

Seasonal variation in the avian community associated with an *Aloe ferox* (Asphodelaceae, Mill.) flowering event in the Eastern Cape, South Africa

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During the winter months in southern Africa the nectar resource that *Aloe* spp. provide represents an important food source for both occasional and true nectarivores in a number of ecosystems. In the Eastern Cape Province, *Aloe ferox* flowers during the dry winter months and offers large volumes of dilute nectar to a variety of bird species. The seasonal variation of the avian community associated with a flowering event of *A. ferox* was investigated at Hounslow Farm north of Grahamstown. Point count sampling at six different stations was conducted over a five month period (April–August 2008) spanning an entire flowering event. Overall, 40 bird species were recorded, 10 of which were classified as occasional nectarivores, and three specialist nectarivores. Significant responses in abundance by both these guilds associated with the increase in nectar availability were recorded. There were no significant changes in species richness during the flowering period which may be attributed to habitat type and/or global nectarivore species richness patterns in the Afrotropical region. The study highlighted the importance of *A. ferox* nectar as an important seasonal food source for a large number of occasional avian nectarivores and one true nectarivore.

INTRODUCTION

The structure and composition of avian communities demonstrate a high degree of spatial and temporal variability that is closely associated with food availability (Brown & Hopkins 1996, Cotton 2006, Franklin & Noske 1999, Gryj *et al.* 1990). Those avian species and communities that make use of ephemeral food sources such as nectar and fruit demonstrate this variation most distinctly (Fleming 1992, Garcia & Ortiz-Pulido 2004, Herrera 1998, Loiselle & Blake 1991). The response of avian nectarivores to variation in food availability has been widely documented and demonstrates the correlation of increased abundance and species diversity associated with an increase in resource availability (Brown & Hopkins 1996, Cotton 2006). For example, frugivorous birds have been shown to track anthropogenic and natural resource variation at a range of spatial scales (Garcia & Ortiz-Pulido 2004, Herrera 1998, Loiselle & Blake 1991). Very similar findings documented by Johnson & Sherry (2001) found that temporal change in arthropod abundance over a short (two weeks) and long-term period (one winter season) was positively correlated with changes in the number of American Redstarts *Setophaga ruticilla* in Jamaica. This trend is also seen in those communities and species that make use of the transient food source, nectar, where an increase in availability is highly correlated with an increase in species richness and abundance (Brown & Hopkins 1996, Cotton 2006, Craig & Hulley 1994, De Swardt 1991, Franklin & Noske 1999, Skead 1967, Symes *et al.* 2001, Tree 1990).

South African examples of true nectarivores demonstrating this correlation include the sunbirds' (Nectariniidae) response to temporarily available nectar resources e.g. *Protea* and *Aloe*

spp. (Craig & Hulley 1994, Craig & Simon 1991, Skead 1967, Symes *et al.* 2001); Gurneys Sugarbird *Promerops gurneyi* (Promeropidae) which responds seasonally to nectar availability (De Swardt 1991, De Swardt & Louw 1994, Symes *et al.* 2001); and the Cape sugarbird *P. cafer* which according to Fraser & McMahon (1992) also demonstrates elevated abundances associated with seasonal flowering of *Protea* spp. Contrasting results were found by Symes *et al.* (2008) who reported the response of the avian community to the nectar resources provided by *Aloe marlothii* in the Gauteng Province (South Africa) to involve a significant increase in abundance and species richness of occasional nectarivores (bulbuls Pycnonotidae, weavers Ploceidae, white-eyes Zosteropidae and mousebirds Coliidae) and not true nectarivores.

In addition to the aforementioned examples describing true nectarivores, there are also widespread cases of occasional nectarivory occurring in a number of avian families across the continents (Maclean 1990). Species defined as occasional nectarivores describe those in feeding guilds other than nectarivore (e.g. frugivore, granivore, insectivore and omnivore) who make use of temporarily available nectar resources. For example, the honeycreepers (Coerebidae), tanagers (Thraupidae) and finches (Fringillidae) in the New World are all classed as occasional nectarivores (Gryj *et al.* 1990). According to Franklin (1999), there are 29 species of insectivores from 15 families found in Australasia that demonstrate occasional nectarivory. Other examples of occasional nectarivory documented in the literature include some generalist passerines (Raju & Rao 2004), as well as non-passerines such as parrots (Psittacidae) (Cotton 2001). During the winter months in southern Africa the nectar resource that *Aloe* spp. provide represents an important food

source for both occasional and true nectarivores in a number of ecosystems (Craig & Hulley 1994, Oatley & Skead 1972, Skead 1967, Symes *et al.* 2001, Symes *et al.* 2008). There are more than 73 bird species in 24 families that have been recorded making use of nectar resources from 14 *Aloe* spp. (Oatley & Skead 1972). *Aloe ferox* (Asphodelaceae, Mill.) is one of the most widely distributed aloe species and occurs from the Swellendam area in the west, to the dry parts of the Western and Eastern Cape Provinces, and southern Kwa-Zulu Natal (Palgrave 2002, Van Wyk & Smith 1996). It occurs in a wide range of habitats; on mountain slopes, both rocky and grassland areas and shows notable adaptability to a range of climates (Hoffman 1988). This species is a robust single-stemmed plant that usually stands 2 m high but may reach a maximum height of 5 m (Palgrave 2002, Van Wyk & Smith 1996). The leaves are broad, dull green and form a compact rosette whilst the stem is densely covered in old dry leaves from previous growing seasons. Flowering occurs from May to August during which plants produce a single inflorescence that is divided into 5–12 erect vertical racemes covered in dense orange-scarlet flowers (Palgrave 2002, Van Wyk & Smith 1996). The racemes are structurally robust and are able to support birds as large as Grey Go-away-birds (*Corythaixoides concolor*) and some columbids (>250 g) (Oatley & Skead 1972). Each flower produces an average of 180 µl of nectar with a concentration of 12.5% w/w (Hoffman 1988).

According to Maclean (1990), nectar production by flowers is an evolutionary adaptation for attracting birds as pollinators; which in turn results in a continued food supply for them as they will guarantee a good seed set. Flowers that are bird pollinated are termed ornithophilous and usually exhibit a broad trend of traits including a red or orange colour, no scent, tubular perianths and abundant dilute nectar (Stiles 1981, Symes & Nicolson 2008). However, recent literature suggests that morphological, physiological and behavioural differences between groups of nectar-feeding birds have led to small-scale variation among those plant groups making use of bird pollinators (Symes & Nicolson 2008). Studies have found a clear divide in bird-pollination systems; the first involves highly specialised nectarivores and the second, a variety of occasional nectarivores (Oatley & Skead 1972, Symes *et al.* 2008, Symes & Nicolson 2008). Flowers adapted for pollination by specialist passerine nectarivores (e.g. sunbirds) have similar nectar properties to those pollinated by hummingbirds (Trochilidae) in terms of volume (approx. 10–30 µl); concentration (approx. 15–25% w/w) and sucrose content (approx. 40–60% of total sugar) (Symes & Nicolson 2008). By contrast, flowers adapted for generalist occasional nectarivore pollination are characterized by large volumes (approx. 40–100 µl) of dilute (approx. 8–12%) nectar with minimal sucrose content (approx. 0–5%).

The inflorescence structure of *A. ferox* (similar to *A. marlothii*) strongly suggests an ornithophilous pollination syndrome in that they have sturdy axes for perching, bright orange to red flowers, long floral tubes, absence of odour and nectar guides, and a long distance between pollen and nectar (Hoffman 1988, Maclean 1990, Stiles 1981, Symes & Nicolson 2008). However, Skead (1967) and Baker (1983) state that pollination may be carried out by more than one pollinator guild. Hoffman's (1988) investigation into the pollination ecology of *A. ferox* found that both insects and birds may be important pollinators and one should not assume a strictly bird-pollinated syndrome based on flower morphology and nectar properties for the species.

The first objective of this study was to investigate the

seasonal variation in the avian community associated with an *A. ferox* flowering event. We predicted that bird abundance, species richness and diversity would increase with an increase in *A. ferox* nectar availability. The second objective of the study was to determine the role of the avian nectarivores in the pollination of *A. ferox*. We also predicted that the occasional nectarivores would have a more significant role to play in their pollination when compared with the true nectarivores.

METHODS

Study site

The study was conducted on Hounsloew Farm (33°11'36.8"S, 26°25'11.9"E) approximately 22 km north-west of Grahamstown, Eastern Cape Province. The sample site encompassed an area of approximately 17.5 ha covering a dense aloe stand (approximately 85 aloes/ha) on a north-facing slope in the Nama-Karoo biome (Mucina & Rutherford 2006). Within this biome, the vegetation type is more specifically described as Albany broken veld which is distributed north of the Zuurberg Mountains and into the area around the confluence of the Great and Little Fish Rivers. It extends eastwards to the Carlisle Bridge area and south into the upper Bushmans river valley (Mucina & Rutherford 2006). The landscape is made up of low mountain ridges and hills covered in open, grassy karroid vegetation with scattered low trees (e.g. *Pappea capensis*, *Euclea undulata*). The groundcover is comprised of a matrix of dwarf shrubs (e.g. *Becium burchellianum*, *Chrysocoma ciliata*) and grasses (e.g. *Eragrostis obtusa*) (Mucina & Rutherford 2006). The geology of the area is comprised mainly of shales and some sandstones within the Cape and Karoo Supergroups (Mucina & Rutherford 2006). The area experiences bimodal rainfall with the main peak in March and the secondary peak in November; however, some rain does fall during the winter months. Mucina & Rutherford (2006) describe *A. ferox* as an important plant taxon within this vegetation type.

Abundance, diversity and community composition

The data were collected over a five month period (April–August 2008) which spanned the autumn non-flowering period (April), the winter flowering period (May–July) and one month after the peak flowering period (August). The point-transect method was employed in this study to sample the avian community (Buckland 2006, Naidoo 2004, Taylor 2007, Toms *et al.* 2006, Willson *et al.* 1973, Willson & Moriarty 1976). According to Bibby *et al.* (1992) and Taylor (2007), this method is capable of detecting more species and is more time efficient and was thus selected over other methods. Six survey stations were randomly placed within the aloe stand with the requirement constraint being they had to be more than 150m apart to ensure the observations were independent (Naidoo 2004, Toms *et al.* 2006). Sampling was carried out twice per month as close to the 10th and 24th of each month depending on the weather conditions. No surveys were undertaken on days when it was windy or raining as these conditions are known to reduce bird activity and/or their detection (Brotons *et al.* 2005, Butler *et al.* 2005, Parker 2008). Each point count sample occurred over a 10 minute period involving an initial two minute wait for any disturbance caused by the observer to dissipate. This allowed bird activity to return to normal (Buckland 2006, Toms *et al.* 2006). This was followed by an eight minute period of sampling. Point counts were carried out three times at each survey station on each

sample day by the same observer (RF); once during each of the following time periods: 06h00–09h00, 11h00–14h00, 15h00–18h00. The observer began the point counts at the same station during each time period each sample day and alternated the start station once a month.

All bird species (seen and heard) excluding raptors, water birds (e.g. ducks, geese and storks) and aerial foragers (e.g. swifts and swallows) within a 30 m radius during the 8-minute period were recorded (Naidoo 2004, Parker 2008, Taylor 2007). Raptors and aerial foragers were excluded as they are often silent and are usually only observed whilst in flight (Naidoo 2004, Parker 2008, Taylor 2007). This makes them difficult to detect and does not allow for an accurate distance to be recorded during point transects (Naidoo 2004, Taylor 2007). Water birds have specific habitat requirements which are not necessarily dictated by the surrounding vegetation (Parker 2008) and were consequently excluded to ensure abundance estimates were not exaggerated (Bibby *et al.* 1992, Taylor 2007). Re-sightings during each point count were not included (Symes *et al.* 2008). The Cape Weaver (*Ploceus capensis*, L.), Village Weaver (*Ploceus cucullatus*, Müller) and Southern Masked Weaver (*Ploceus velatus*, Vieillot) were treated as one morpho-species due to difficulties in identifying birds in non-breeding plumage (Parker 2008, Taylor 2007).

Data collected included survey station number, time period, species, number of individuals, and distance (m) from point-to-bird. Any feeding behaviour pertaining to the aloes during the flowering season was also recorded (i.e. probing flowers; feeding on buds, open flowers or seed pods) (Symes *et al.* 2008). Those bird species observed feeding on *A. ferox* nectar were classified into two guilds; specialist (e.g. sunbirds) or occasional nectarivores (e.g. starlings and weavers). Specialist nectarivores were defined as those species that fed primarily on nectar and had the necessary morphological adaptations (bill shape) for obtaining it (Maclean 1990, Oatley 1964). Occasional nectarivores were defined as those species observed feeding on nectar during the point count surveys which didn't have any specialist adaptations for obtaining the food source (i.e. were not specialist nectarivores but were observed feeding on nectar) (Maclean 1990). All bird species were categorised as seasonal migrants or not. The distance from point-to-bird was measured to a point vertically below the bird (using a Nikon Laser 800S rangefinder) and not the bird itself to ensure more accurate measurements (Buckland 2006, Parker 2008). Birds detected audibly were placed in 10m distance intervals from the observer (Parker 2008, Taylor 2007). The family, common and scientific names of all bird species recorded during the course of this study during point counts and on the study site are provided in Appendix I (Taxonomy follows Hockey *et al.* 2005).

Role in pollination

The marking and subsequent monitoring of individual birds is important to understand survivorship, movement and other aspects of ecology such as their role in plant-pollination (Pollock & Paxton 2006, White & Burnham 1999). Mist nets have long been a successful tool for capturing certain passerines and are the only effective method for many species (Bibby *et al.* 1992, Bub 1978, Pollock & Paxton 2006). To better evaluate the pollinating roles of various bird species, the presence of *A. ferox* pollen on those birds feeding on the aloe flowers was used as an indicator of the role that species may play in the pollination of the plant (Hargreaves *et al.* 2004). To determine the presence of *A. ferox* pollen on birds

feeding on the aloe flowers (Borgella *et al.* 2001, Hargreaves *et al.* 2004, Johnson & Brown 2004, Noske 1993, Symes *et al.* 2008), they were trapped using mist nets (Bibby *et al.* 1992, Pollock & Paxton 2006, Symes *et al.* 2008, Willson & Moriarty 1976). Two sets of four individual mist nets (12 × 2.4 m, 4 shelf, 16 mm mesh) were erected (0.4–2.8 m) on aluminium poles (3 m) at two separate localities within the study site forming two continuous nets of 48 m. Nets were erected between 07h30 and 08h00 for a consistent 8 hour period on each sample day resulting in a total of 80 net-hours over the five-month sampling period. Each bird caught was ringed and inspected for pollen deposited on the bill and feathers of the facial region with the naked eye. The number of individuals with pollen present was converted to a percentage of all individuals of that species caught during the flowering period. Data for this analysis included the total frequency of all species caught over the flowering period. (The weaver morpho-species used during point counts did not apply here as all weavers were identified to species level.)

Flowering period

In order to quantify when peak flowering occurred all aloes within a 10 m radius of each survey station were counted (n = 124). Each aloe was placed into one of three categories; budding, flowering or inactive. The same aloes were classified into their respective categories (depending on what flowering state they were in) each sample day. The 'budding' state described an aloe with greenish-yellow flowers present on the raceme(s) which were still closed. The 'flowering' state described an aloe with orange-red flowers present on the raceme(s) which had opened and exposed the pollen-covered stamens. The 'inactive' state described an aloe that had either not produced any racemes this season or one that had passed through the flowering period and now had seeds on the raceme(s).

Data analysis

The differences between monthly means of abundance of all individuals, true nectarivores, occasional nectarivores; and species richness were statistically analysed using a one-way ANOVA after ensuring the data were normally distributed using the Kolmogorov–Smirnov, Lilliefors and Shapiro–Wilks tests (Statistica vers.8). A post-hoc Tukey's test was performed to determine which months were significantly differently from others (Statistica vers.8). Regression analyses were performed to determine the relationship between the abundance of all birds and true nectarivores, and the percentage of aloes that were flowering (flowering period) (Statistica vers.8). The Shannon–Wiener diversity index (H') was determined per month using the programme Estimate STM to illustrate the evenness of species occurring within the community (Borgella *et al.* 2001, Hurlbert 1971, Karr & Roth 1971, Tramer 1969, Willson & Moriarty 1976). Data for this analysis included all observations of each species per month.

RESULTS

Flowering period

All aloes that flowered during the sampling period produced a single set of racemes with the first inflorescences (buds) visible at the beginning of May (Fig. 1). Peak budding occurred at the beginning of June with 60% of all aloes in the sampled area containing buds. The first flowers opened at the end

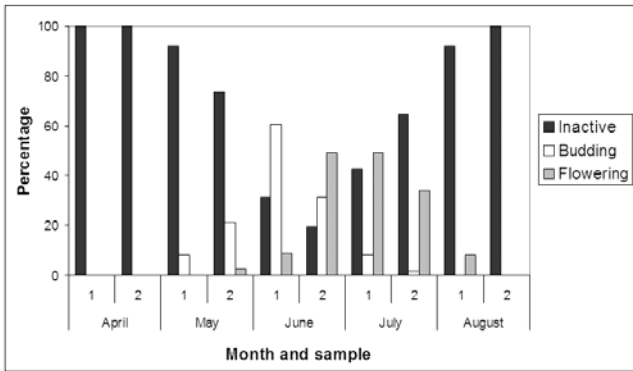


Fig. 1. The percentage of aloes (n = 124) in the described states (inactive, budding or flowering) on each sample day during the five-month sampling period (April–August 2008).

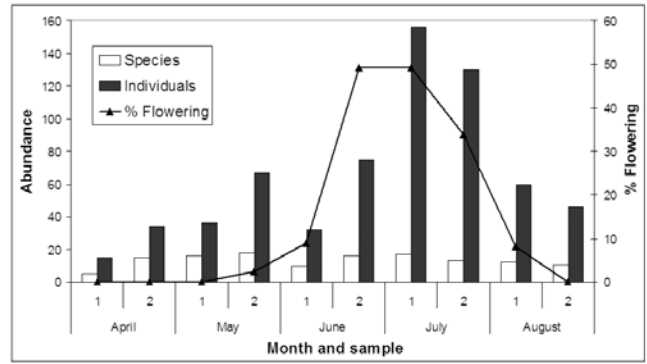


Fig. 2. The abundance of all birds and species per sample, and the percentage of aloes in a flowering state during the five-month sampling period (April–August 2008).

of May and by early August flowering was complete. Peak flowering occurred at the end of June and continued through to the beginning of July with 49% of all aloes in the sampled area (n = 124) in a flowering state (Fig. 1).

Abundance, diversity and community composition

A total of 40 bird species was observed during the entire sampling period (Appendix I). No seasonal migrants were observed during any of the months. The abundance of individuals observed increased steadily from the first sample in April to a peak at the beginning of July (Fig. 2). A low at the beginning of June was also recorded. This was followed by a steady decline towards the end of August. The increase in abundance tracked the increasing number of aloes in flower (% flowering). There was a clear delayed response to the peak availability of nectar seen at the beginning of July (Fig. 2). The monthly mean abundance of all birds in July was significantly higher than all other months ($p < 0.05$, $F_{4,5} = 10.12$); all other months showed no significant differences. The number of species observed throughout the sampling period remained relatively similar with the maximum number of species observed during the first May sample. No significant differences were found between monthly means of species richness ($p = 0.49$, $F_{4,5} = 0.98$).

The community composition shows a clear shift tracking the number of flowering aloes (Fig. 3). The abundance of *occasional* and *true* nectarivores increased steadily towards July tracking the increase in the number of flowering aloes

(Fig. 3). This was followed by a steady decline in the abundance of both guilds. The number of *other birds* (those not classified as occasional or true nectarivores) observed remained relatively unchanged throughout the sampling period. Significant differences were found between the monthly mean abundance of true nectarivores ($p < 0.05$, $F_{4,5} = 31.65$) and occasional nectarivores ($p < 0.05$, $F_{4,5} = 5.31$) with the highest abundance of each guild recorded during July.

There was a significant relationship between the percentage of aloes in flower and the abundance of all birds on the study site with 61% of the variability in their abundance being explained by the percentage of aloes in flower ($p < 0.05$, $R^2 = 0.61$). A significant relationship between the percentage of aloes in flower and the abundance of occasional nectarivores was found with 44% of the variability in their abundance being explained by the percentage of aloes in flower ($p < 0.05$, $R^2 = 0.68$). There was a significant relationship between the percentage of aloes in flower and the abundance of true nectarivores on the study site with 68% of the variability in their abundance being explained by the percentage of aloes in flower ($p < 0.05$, $R^2 = 0.68$) (Fig. 4).

The cumulative species richness per month ranged from 16 species (April and August) to 26 species (May) (Table 1). The monthly Shannon–Wiener diversity indices illustrate the highest evenness during May (2.97) and the lowest observed during the peak flowering period (June – 1.97 and July – 1.66) (Table 1).

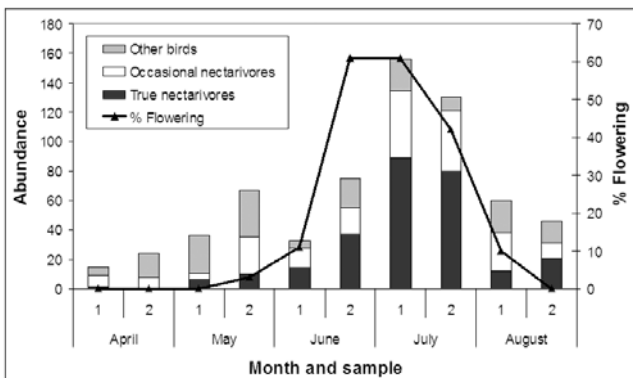


Fig. 3. All bird abundance partitioned into *occasional* and *true* nectarivores, and *other birds* over the five-month sampling period (April–August 2008) in relation to the percentage of flowering *A. ferox*.

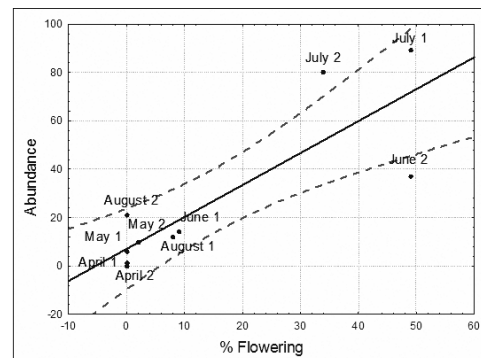


Fig. 4. Scatter plot showing the significant ($p < 0.05$, $R^2 = 0.68$) relationship between the abundance of *true nectarivores* and the percentage of flowering aloes. (Solid line indicates the linear relationship; dotted lines indicate 95% confidence interval).

Role in pollination

Out of the 11 species of occasional nectarivore (Appendix II) observed in this study, seven were caught in the mist nets; two of which (Cape Weaver and Streaky-headed Seedeater) regularly had pollen on the bill and/or plumage in the facial region (Table 2). Eighty-one percent of all Cape Weavers ($n = 53$) and 50% of all Streaky-headed Seedeaters caught ($n = 8$) had pollen in this region. Two of the three species of true nectarivore observed in this study (Appendix II) were captured (Malachite Sunbird and Southern Double-collared Sunbird *Cinnyris chalybeus*). Ten percent ($n = 10$) of all Malachite Sunbirds caught showed pollen deposited on their plumage, while the only ($n = 1$) Southern Double-collared Sunbird caught did not have any pollen on it (Table 2).

DISCUSSION

Nectar-feeding at a mass flowering event

The flowering period of *A. ferox* observed in this study is in agreement with the literature describing the duration and onset of the flowering period occurring from May to August with peak flowering occurring during mid-winter (Hoffman 1988, Palgrave 2002, Van Wyk & Smith 1996). The significant increase in the number of birds during the flowering stage indicates that *A. ferox* nectar is an important food source during this dry winter period. The data thus support the hypothesis that bird abundance would increase with an increase in the availability of *A. ferox* nectar. On a broader scale, the increase in abundance associated with an increase in resource availability documented here mirrors those studies reporting similar trends in the cases of avian frugivores and insectivores (Fleming 1992, Herrera 1998, Johnson & Sherry 2001, Loiselle & Blake 1991, Garcia & Ortiz-Pulido 2004). The significant increase in occasional and true nectarivores tracking the increase in nectar availability also supports the general trend in studies investigating avian nectarivores (Brown & Hopkins 1996, Cotton 2006, De Swardt 1991, Franklin & Noske 1999, Gryj *et al.* 1990, Skead 1967, Symes *et al.* 2001). This was highlighted by certain species only being present during the flowering period e.g. Streaky-headed Seedeater, Malachite Sunbird and Red-winged Starling *Onychognathus morio* which are known to move extensively while tracking food resources (Fraser 1997, Skead 1967, Symes *et al.* 2001). The significant increase in abundance of true nectarivores recorded did not match the findings of Symes *et al.* (2008) who documented no significant response by the true nectarivores (sunbirds) to the seasonal availability of *A. marlothii* nectar at Suikerbosrand Nature Reserve in the Gauteng Province, South Africa. The relationship between the percentage of aloes in flower and the abundance of all birds, and true nectarivores was stronger when compared with the abundance of occasional nectarivores. The weaker relationship between the occasional nectarivores and percentage flowering means there are other factors influencing their abundance in addition to the presence of the *A. ferox* nectar resource. These factors may include the availability of other food resources such as insects or fruit and the availability of nesting sites. However, by definition, species within this guild are not dependent on the nectar resources for food as they are occasional nectarivores which make use of ephemeral food sources when they are available. Thus the relationship between them and the percentage of flowering aloes is not expected to be a strong one.

The monthly cumulative species richness did not track the availability of nectar which does not support the hypothesis of increased species richness associated with increased nectar availability. A possible explanation for the peak species richness in May (26 species) may be the appearance of the first buds at the beginning of that month, and the first flowers at the end of the month providing a new food source. The Streaky-headed Seedeater and the Malachite Sunbird both arrived shortly after the aloes began to bud. In addition, the weather on both sampling days during May was exceptionally good with minimal wind allowing for greatest bird activity, and conditions may have increased the probability of detection by the observer (Brotons *et al.* 2005, Butler *et al.* 2005, Parker 2008). The relative lows of 16 species recorded during April and August may be attributed to the aloes having not begun (April) or finished (August) the flowering season. These findings contrast with other studies reporting increases in nectarivorous species richness associated with: rainforest flower resources in New Guinea (Brown & Hopkins 1996); flowering plants in monsoonal woodland near Darwin, Australia (Franklin & Noske 1999); flowering resources in the Amazon, Columbia (Cotton 2006) and flowering *A. marlothii* in grassland-savannah, South Africa (Symes *et al.* 2008). The habitat type may have influenced the lack of change in species richness in that there may be fewer species which make use of ephemeral nectar resources in the Nama-Karoo biome when compared with other habitat types such as those previously mentioned. The second hypothesis is that these patterns are part of a broader scale phenomenon reflecting global variation in avian nectarivore species richness where the Neotropical (324 hummingbird species) and Australasian (159 honeyeaters) regions have more speciose nectarivore radiations when compared with the Afrotropical (78 sunbirds and 2 sugarbirds) and Indomalayan (39 sunbirds and 10 honeyeaters) regions (Maclean 1990, Symes *et al.* 2008).

When comparing the Shannon-Wiener diversity indices between months, the data did not support the hypothesis that

Table 1. Cumulative species richness and Shannon–Wiener diversity index (H') per month over the five-month sampling period.

Month	Cumulative species richness	Shannon–Wiener diversity index (H')
April	16	2.46
May	26	2.97
June	21	1.97
July	22	1.66
August	16	2.17

Table 2. The percentage of individuals of each species caught in the mist nets, classified as either *true nectarivores* or *occasional nectarivores*, with pollen present on their bill or plumage in the facial region during the flowering period (May–August 2008).

Guild	Species	n	Percentage with pollen present (%)
True nectarivore	Malachite Sunbird	10	10
	Southern Double-collared Sunbird	1	0
Occasional nectarivore	Cape Weaver	53	81
	Streaky-headed Seedeater	8	50

diversity would increase with an increase in nectar availability. However, the lack of evenness observed during the peak flowering period (June–July) may be attributed to the arrival of one species *en masse*, the Malachite Sunbird. The abundance of this species accounted for between 50 and 58% of the total bird abundance recorded during this time period, which resulted in the evenness being considerably skewed.

Role in pollination

Hoffman's (1988) investigation into the pollination ecology of *A. ferox* found that although its inflorescence structure suggests an ornithophilous pollination syndrome, it was instead a combination of insects and birds which were responsible for its pollination. We tried to determine which guild of birds, either occasional or true nectarivore, played a more significant role in its pollination. Our findings clearly show that the occasional nectarivores, specifically the Cape Weaver and Streaky-headed Seedeater, play a considerably larger role in the pollination of *A. ferox* compared with the true nectarivores. According to Symes & Nicolson (2008) flowers adapted for pollination by specialist nectarivores produce small amounts (approx. 10–30 µl) of relatively high concentrated (approx. 15–25% w/w) nectar with a high sucrose content (approx. 40–60% of total sugar), whilst flowers adapted for generalist occasional nectarivore pollination are characterized by large volumes (approx. 40–100 ml) of dilute (approx. 8–12%) nectar with minimal sucrose content (approx. 0–5%). The data here, suggesting occasional nectarivores have a larger role to play in the pollination of *A. ferox*, support these ideas in that the high volume (180 µl) and low sucrose concentration (12.5%) of *A. ferox* nectar (Hoffman 1988) fit the description of a generalist pollination syndrome. This is supported by Symes *et al.* (2008) who found a significant response by occasional nectarivores to the flowering of *A. marlothii* which has very similar nectar properties (250 µl, 12% concentration) and inflorescence structure (yellowy-red colour, no scent, sturdy perching axes) to *A. ferox* indicating the larger role of occasional nectarivores in the pollination of these two species.

Future scope

Future field research should investigate the relationship between aloe plant density and bird abundance; we would expect that sites with higher aloe densities will attract higher bird abundances. There is also broad scope for exploring the pollination ecology of these plants and determining the relative significance of insects and birds in their pollination (Hoffman 1988, Human & Nicolson 2008, Symes & Nicolson 2008). In addition, it is crucial to ensure the scales on which studies are carried out are appropriate for the research question. According to Fleming (1992) no bird moves around aimlessly in the hope of encountering a food source but rather tracks resources to maximise their fitness. When relating this to nectarivore abundance associated with nectar availability, the research question should be “At what spatio-temporal scale(s) are they correlated?” (Franklin & Noske 1999). For avian nectarivores, processes such as these tend to operate at larger scales than are generally practical to study and thus this survey may need to be repeated at a larger spatial (more sites) and temporal (more flowering seasons) scale in order to gain a more accurate understanding of the changes in abundance and species richness of avian nectarivores associated with *A. ferox* flowering events.

Conclusion

The avian community changes observed related to the increase in *A. ferox* nectar availability highlight the importance of this resource for a large number of individuals and one particular true nectarivore. This supports the general trend in the literature in both local regions and on other continents. However, the lack of any significant changes in species richness associated with the increase in *A. ferox* nectar availability is in contrast to other studies. Potential explanations for this include the possible effects of habitat type and the associated different suites and numbers of species; and/or the presence of relatively few specialist nectarivores in this region (Afrotropical) compared with other regions (Neotropical and Australasian) (Maclean 1990). The dry winter season in the Eastern Cape is thus a period of predictable and abundant *A. ferox* nectar resources. In addition, it is also a period when many other resources such as fruit and insects may be in short supply. The combination of these circumstances has major ramifications for the survival and behaviour of avian nectarivores in the Eastern Cape Province which need to be explored further. The evidence that occasional nectarivores play a more significant role in the pollination of *A. ferox* on the study site compared with the true nectarivores demonstrates that this aloe has a generalist pollination syndrome, as found in a previous study on its pollination ecology (Hoffman 1988). Although floral syndromes can lead to accurate predictions about the effective pollinators of certain plant species (Hargreaves *et al.* 2004), it should not be advocated that syndromes be accepted as evidence that a plant is pollinated by a particular species or guild of species. Thus although *A. ferox* is ornithophilous, the guild of birds pollinating it were not specialists but rather generalists, which is not specified by its “ornithophilous” pollination syndrome description.

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REFERENCES

- Baker, H.G. 1983. An outline of the history of anthecology, or pollination biology. In: Real, L. (ed.) *Pollination biology*. Academic Press, Orlando, Florida, USA. pp. 7–28.
- Bibby, C.J., Burgess, N.D., Hill, D.A. & Mustoe, S.H. 2000. *Bird census techniques* (2nd ed.) Academic Press, London, United Kingdom.
- Borgella Jr., R., Snow, A.A. & Gavin, T.A. 2001. Species richness and pollen loads of hummingbirds using forest fragments in Southern Costa Rica. *Biotropica* 33: 90–109.
- Brotons, L., Wolff, A., Paulus, G. & Martin, J.L. 2005. Effect of adjacent agricultural habitat on the distribution of passerines in natural grasslands. *Biological Conservation* 124: 407–414.
- Brown, E.D. & Hopkins, M.J.G. 1996. How New Guinea rainforest flower resources vary in time and space: implications for nectarivorous birds. *Australian Journal of Ecology* 21: 363–378.
- Bub, H. 1978. *Bird trapping and bird banding: A handbook for trapping methods all over the world*. Cornell University Press, New York.
- Buckland, S.T. 2006. Point transect surveys for songbirds: robust methodologies. *Auk* 123: 345–357.
- Butler, S.J., Bradbury, R.B. & Whittingham, M.J. 2005. Stubble height affects the use of stubble fields by farmland birds. *Journal of Applied Ecology* 42: 469–476.
- Cotton, P.A. 2001. The behaviour and interactions of birds visiting *Erythrina fusca* flowers in the Columbian Amazon. *Biotropica* 33: 662–669.
- Cotton, P.A. 2006. Seasonal resource tracking by Amazonian hummingbirds. *Ibis* 149: 135–142.

- Craig, A.J.F.K. & Hulley, P.E. 1994. Sunbird movements: a review with possible models. *Ostrich* 65: 106–110.
- Craig, A.J.F.K. & Simon, C.A. 1991. Sunbird and sugarbird seasons. *Safring News* 20: 9–12.
- De Swardt, D.H. 1991. The seasonal movements of Gurney's Sugarbird *Promerops gurneyi* in the Lydenburg area, Transvaal. *Ostrich* 62: 40–44.
- De Swardt, D.H. & Louw, S. 1994. The diet and foraging behaviour of Gurney's Sugarbird *Promerops gurneyi*. *Navorsing van die Nasionale Museum Bloemfontein* 10: 245–258.
- Fleming, T.H. 1992. How do fruit- and nectar-feeding birds and mammals track their food resources? In: Hunter, M.D., Ohgushi, T., Price, P.W. (eds). *Effects of resource distribution on animal-plant interactions*. Academic Press, San Diego, pp 355–391.
- Franklin, D.C. 1999. Opportunistic nectarivory: an annual dry season phenomenon among birds in monsoonal northern Australia. *Emu* 99: 135–141.
- Franklin, D.C. & Noske, R.A. 1999. Birds and nectar in a monsoonal woodland: correlations at three spatio-temporal scales. *Emu* 99: 15–28.
- Fraser, M.W. 1997. Malachite Sunbird *Nectarinia famosa*. In: Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V., Brown, C.J. (eds). *The atlas of Southern African birds vol 2: Passerines*. BirdLife South Africa, Johannesburg, pp. 488–490.
- Fraser, M.W. & McMahon, L. 1992. Habitat change by Cape Sugarbirds and Orangebreasted Sunbirds in an apparent response to fire in old mountain fynbos. *Safring News* 21: 51–54.
- Garcia, D. & Ortiz-Pulido, R. 2004. Patterns of resource tracking by avian frugivores at multiple spatial scales: two case studies on discordance among scales. *Ecography* 27: 187–196.
- Gryj, E., Martinez del Rio, C. & Baker, E. 1990. Avian pollination and nectar use in *Combretum fruticosum* (Loefl). *Biotropica* 22: 266–271.
- Hargreaves, A.L., Johnson, S.D. & Nol, E. 2004. Do floral syndromes predict specialisation in plant pollination systems? An experimental test in an "ornithophilous" African *Protea*. *Oecologia* 140: 295–301.
- Herrera, C.M. 1998. Long-term dynamics of Mediterranean frugivorous birds and fleshy-fruits: a 12-year study. *Ecological Monographs* 68: 511–538.
- Hockey, P.A.R., Dean, W.R.J. & Ryan, P.G. 2005. *Roberts – Birds of southern Africa*, (7th ed.). The Trustees of the John Voelcker Bird Book Fund, Cape Town.
- Hoffman, M.T. 1988. The pollination ecology of *Aloe ferox* Mill. *South African Journal of Botany* 54: 345–350.
- Human, H. & Nicolson, S.W. 2008. Flower structure and nectar availability in *Aloe greatheadii* var. *davyana*: An evaluation of a winter nectar source for Honeybees. *International Journal of Plant Sciences*. 169: 263–269.
- Hurlbert, S.H. 1971. The nonconcept of species diversity: a critique and alternative parameters. *Ecology* 52: 577–586.
- Johnson, S.D. & Brown, M. 2004. Transfer of pollen on birds' feet: a new pollination system in orchids. *Plant Systematics and Evolution* 244: 181–188.
- Johnson, M.D. & Sherry, T.W. 2001. Effects of food availability on the distribution of migratory warblers among habitats in Jamaica. *Journal of Animal Ecology* 70: 546–560.
- Karr, J.R. & Roth, R.R. 1971. Vegetation structure and avian diversity in several New World areas. *American Naturalist* 105: 423–435.
- Loiselle, B.A. & Blake, J.G. 1991. Temporal variation in birds and fruits along an elevational gradient in Costa Rica. *Ecology* 72: 180–193.
- Maclean, G.L. 1990. *Ornithology for Africa*. University of Natal Press, Pietermaritzburg.
- Mucina, L. & Rutherford, M.C. (eds). 2006. The vegetation of South Africa, Lesotho and Swaziland. *Strelitzia* 19. South African National Biodiversity Institute, Pretoria.
- Naidoo, R. 2004. Species richness and community composition of songbirds in a tropical forest-agricultural landscape. *Animal Conservation* 7: 93–105.
- Noske, R.A. 1993. *Bruguiera hainesii*: Another bird-pollinated mangrove? *Biotropica* 25: 481–483.
- Oatley, T.B. 1964. The probing of Aloe flowers by birds. *Lammergeyer* 3: 2–8.
- Oatley, T.B. & Skead, D.M. 1972. Nectar-feeding by South African birds. *Lammergeyer* 15: 68–69.
- Palgrave, K.C. 2002. *Trees of Southern Africa* (3rd ed.). Struik Publishing, Cape Town.
- Parker, D.M. 2008. *The effects of elephants at low densities and after short occupation time on the ecosystems of the Eastern Cape Province, South Africa*. Unpublished Phd thesis, Rhodes University, Grahamstown, South Africa.
- Pollock, M.G. & Paxton, E.H. 2006. Floating mist nets: a technique for capturing birds in flooded habitat. *Journal of Field Ornithology* 77: 335–338.
- Raju, A.J.S. & Rao, S.P. 2004. Passerine bird pollination and fruiting behaviour in a dry season blooming tree species *Erythrina suberosa* Roxb. (Fabaceae) in the Eastern Ghats forests India. *Ornithological Science* 3: 139–144.
- Skead, C.J. 1967. *The sunbirds of southern Africa*. Balkema, Cape Town, South Africa.
- Stiles, F.G. 1981. Geographical aspects of bird-flower coevolution, with particular reference to Central America. *Annals of the Missouri Botanical Garden* 68: 323–351.
- Symes, C.T. & Nicolson, S.W. 2008. (In press) Production of copious dilute nectar in the bird-pollinated succulent *Aloe marlothii* (Asphodelaceae). *South African Journal of Botany*.
- Symes, C.T., Downs, C.T. & McLean, S. 2001. Seasonal occurrence of the Malachite Sunbird *Nectarinia famosa* and Gurney's Sugarbird *Promerops gurneyi* in KwaZulu-Natal South Africa. *Ostrich* 72: 45–49.
- Symes, C.T., Nicolson, S.W. & McKechnie, A.E. 2008. Response of avian nectarivores to the flowering of *Aloe marlothii*: a nectar oasis during dry South African winters. *Journal of Ornithology* 149: 13–22.
- Taylor, M.R. 2007. *An evaluation of bird presence and breeding captivity in regenerating coastal dune forests, Maputaland, South Africa*. Unpublished M.Sc. Thesis, University of Pretoria, Pretoria.
- Toms, J.D., Schmiegelow, F.K.A., Hannon, S.J. & Villard, M.A. 2006. Are point counts of boreal songbirds reliable proxies for more intensive abundance estimators? *Auk* 123: 438–454.
- Tramer, E.J. 1969. Bird species diversity: components of Shannon's formula. *Ecology* 50: 927–929.
- Tree, A.J. 1990. Notes on sunbird movements and nectar sources in Zimbabwe. *Honeyguide* 36: 171–182.
- Van Wyk, B.E. & Smith, G. 1996. *Guide to the Aloes of South Africa*. Briza Publications, Pretoria.
- White, G.C. & Burnham, K.P. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46: 120–138.
- Willson, M.F. & Moriarty, D.J. 1976. Bird species diversity in forest understorey: Analysis of mist-net samples. *Oecologia* 25: 373–379.
- Willson, M.F., Anderson, S.H. & Murray, B.G. 1973. Tropical and temperate species diversity: within-habitat and between-habitat comparisons. *Caribbean Journal of Sciences* 13: 81–90.

APPENDIX I

Bird species recorded during point counts (April–August 2008) in an *Aloe ferox* stand on the Hounslow Farm, Eastern Cape Province.

Species	Nectar	Status	Apr	May	Jun	Jul	Aug	Total
Numididae								
Helmeted Guineafowl <i>Numida meleagris</i>		<i>o</i>						
Anatidae								
South African Shelduck <i>Tadorna cana</i>		<i>o</i>						
Picidae								
Red-throated Wryneck <i>Jynx ruficollis</i>		<i>c</i>	-	1	1	-	-	2
Lybiidae								
Acacia Pied Barbet <i>Tricholaema leucomelas</i>		<i>c</i>	5	4	1	1	1	12
Black-collared Barbet <i>Lybius torquatus</i>		<i>o</i>						
Red-fronted Tinkerbird <i>Pogoniulus pusillus</i>		<i>o</i>						
Dacelonidae								
Brown-hooded Kingfisher <i>Halcyon albiventris</i>		<i>o</i>						
Coliidae								
Speckled Mousebird <i>Colinus striatus</i>			-	-	-	2	-	2
Red-faced Mousebird <i>Urocolius indicus</i>		<i>c</i>	-	9	1	7	14	31
Columbidae								
Speckled Pigeon <i>Columba guinea</i>		<i>tr</i>	-	1	-	-	-	1
Laughing Dove <i>Sreptopelia enegalensis</i>		<i>c</i>	1	6	1	2	-	10
Cape Turtle Dove <i>Sreptopelia capicola</i>		<i>o, c</i>						
Accipitridae								
Pale Chanting Goshawk <i>Melierax canorus</i>		<i>o</i>						
Booted Eagle <i>Aquila pennatus</i>		<i>o, mig</i>						
Falconidae								
Lanner Falcon <i>Falco biarmicus</i>		<i>o</i>						
Threskiornithidae								
Hadeda Ibis <i>Bostrychia hagedash</i>		<i>o</i>						
Oriolidae								
Black-headed Oriole <i>Oriolus larvatus</i>		<i>o</i>						

Abundance (total number) of birds indicated. ^a indicates the morpho-species Weaver abundance. Nectar: *f* feeding on nectar or not, *p* pollen recorded on bird. Status: *tr* transient fly over; *mig* migrant or not, *o* observed on site not during point counts, *c* caught in mist nets.

APPENDIX I continued

Species	Nectar	Status	Apr	May	Jun	Jul	Aug	Total
Dicruridae								
Fork-tailed Drongo <i>Dicrurus adsimilis</i>	<i>f</i>		-	-	1	-	-	1
Malacoenotidae								
Southern Tchagra <i>Tchagra tchagra</i>		<i>o</i>						
Bokmakierie <i>Telophorus zeylonus</i>		<i>o</i>						
Greyheaded Bush-Shrike <i>Malacoenotus blanchoti</i>		<i>c</i>						
Corvidae								
Cape Crow <i>Corvus capensis</i>		<i>tr</i>	1	-	-	-	-	1
White-necked Raven <i>Corvus albicollis</i>		<i>tr</i>				3	1	4
Laniidae								
Common Fiscal <i>Lanius collaris</i>			-	1	1	1	-	3
Paridae								
Cape Penduline Tit <i>Anthoscopus minutus</i>			-	4	-	-	-	4
Grey Tit <i>Parus afer</i>		<i>o</i>						
Pycnonotidae								
Dark-capped Bulbul <i>Pycnonotus tricolor</i>	<i>f</i>	<i>c</i>	2	6	4	5	5	22
Sombre Greenbul <i>Andropadus importunus</i>		<i>c</i>	-	-	1	-	-	1
Sylviidae								
Long-billed Crombec <i>Sylvietta rufescens</i>		<i>c</i>	1	4	1	-	1	7
Chestnut-vented Tit-Babbler <i>Parisoma subcaeruleum</i>			1	1	2	-	1	5
Zosteropidae								
Cape White-eye <i>Zosterops virens</i>	<i>f</i>		-	-	-	4	-	4
Cisticolidae								
Grey-backed Cisticola <i>Cisticola subruficapilla</i>		<i>o, c</i>						
Neddicky Cisticola <i>fulvicapilla</i>		<i>c</i>	9	5	3	4	3	24
Karoo Prinia <i>Prinia maculosa</i>	<i>f</i>	<i>c</i>	9	6	9	4	3	31
Bar-throated Apalis <i>Apalis thoracica</i>		<i>c</i>	-	1	-	-	-	1
Muscicapidae								
Cape Rock-Thrush <i>Monticola rupestris</i>	<i>f</i>	<i>c</i>	1	1	-	-	1	3
Fiscal Flycatcher <i>Sigelus silens</i>		<i>c</i>	2	2	-	1	1	6
Cape Robin-Chat <i>Cossypha caffra</i>			-	-	-	1	-	1

APPENDIX I continued

Species	Nectar Status	Apr	May	Jun	Jul	Aug	Total
White-browed Scrub-Robin	c	2	-	-	-	-	2
<i>Cercotrichas leucophrys</i>							
Karoo Scrub-Robin		4	7	4	-	2	17
<i>Cercotrichas coryphaeus</i>							
Familiar Chat <i>Cercomela familiaris</i>		2	3	1	6	5	17
Anteating Chat <i>Myrmecocichla formicivora</i>		-	1	-	-	-	1
Sturnidae							
Red-winged Starling	f, p	-	-	-	4	-	4
<i>Onychognathus morio</i>							
Cape Glossy Starling	f, p	-	-	-	3	-	3
<i>Lamprotornis nitens</i>							
Pied Starling <i>Spreo bicolor</i>	f	-	-	-	1	-	1
Nectariniidae							
Amethyst Sunbird	tr	1	1	-	-	-	2
<i>Chalcomitra amethystina</i>							
Malachite Sunbird <i>Nectarinia famosa</i>	f, p	-	12	53	166	33	264
Southern Double-collared Sunbird	p	c					
<i>Cinnyris chalybeus</i>							
Greater Double-collared Sunbird	f	-	3	2	3	-	8
<i>Cinnyris afer</i>							
Ploceidae							
Weaver ^a	f, p	c	5	6	4	38	10

Abundance (total number) of birds indicated. ^a indicates the morpho-species Weaver abundance. Nectar: f feeding on nectar or not, p pollen recorded on bird. Status: tr transient fly over; mig migrant or not, o observed on site not during point counts, c caught in mist nets.

APPENDIX I continued

Species	Nectar Status	Apr	May	Jun	Jul	Aug	Total
Southern Masked Weaver	c						
<i>Ploceus velatus</i>							
Village Weaver <i>Ploceus cucullatus</i>	c						
Cape Weaver <i>Ploceus capensis</i>	f, p	c					
Red-billed Quelea <i>Quelea quelea</i>	c, mig						
Estrildidae							
Common Waxbill <i>Estrilda astrild</i>		-	-	-	3	-	3
Passeridae							
Cape Sparrow <i>Passer melanurus</i>		3	1	2	-	-	6
Southern Grey-headed Sparrow	c	-	-	1	-	-	1
<i>Passer diffusus</i>							
Yellow-throated Petronia	f	c	-	-	1	2	3
<i>Petronia supercilii</i>							
Motacillidae							
Cape Wagtail <i>Motacilla capensis</i>	o						
Fringillidae							
Cape Canary <i>Serinus canicollis</i>		-	2	-	-	-	2
Yellow-fronted Canary		-	2	-	-	-	2
<i>Crithagra mozambica</i>							
Streaky-headed Seedeater	f	c	-	13	25	17	68
<i>Crithagra gularis</i>							
Cape Bunting <i>Emberiza capensis</i>	o						

APPENDIX II.

Bird species recorded during point counts (April - August 2008) classified as either occasional or true nectarivores.

Occasional nectarivore	True nectarivore
Dicruridae: Fork-tailed Drongo <i>Dicrurus adsimilis</i>	Nectariniidae: Amethyst Sunbird <i>Chalcomitra amethystina</i>
Pycnonotidae: Dark-capped Bulbul <i>Pycnonotus tricolor</i>	Malachite Sunbird <i>Nectarinia famosa</i>
Zosteropidae: Cape White-eye <i>Zosterops virens</i>	Greater Double-collared Sunbird <i>Cinnyris afer</i>
Cisticolidae: Karoo Prinia <i>Prinia maculosa</i>	
Muscicapidae: Cape Rock-Thrush <i>Monticola rupestris</i>	
Sturnidae: Redwinged Starling <i>Onychognathus morio</i>	
Cape Glossy Starling <i>Lamprotornis nitens</i>	
Pied Starling <i>Spreo bicolor</i>	
Ploceidae: Cape Weaver <i>Ploceus capensis</i>	
Fringillidae: Streaky-headed seedeater <i>Crithagra gularis</i>	
Passeridae: Yellow-throated Petronia <i>Petronia supercilii</i>	