



Specialist and generalist avian nectarivores co-dominate visitation to a summer-flowering grassland aloe

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ABSTRACT

Aloe reitzii var. *reitzii* is a summer-flowering (February–March) succulent, endemic to a restricted range within the heavily transformed grasslands of eastern South Africa. Floral structure and nectar properties suggest bird-pollination. This study investigated the temporal visitation events of birds to this aloe. Extensive camera observations during the 2017 flowering season (23 days) identified both specialist and generalist nectarivorous birds ($n =$ four and five species respectively) as regular diurnal aloe visitors. Malachite Sunbirds (*Nectarinia famosa*) accounted for 49% of all visits, while Cape Weavers (*Ploceus capensis*) made up 41% of all visits; these species co-dominate visitation of the specialist and generalist avian feeding guilds respectively. In addition, visitation by each guild was separated temporally to some extent, with generalists mostly visiting early in the day, while specialists dominate afternoon visitation. Nectar volume (overall unbagged mean = $48.67 \pm 4.70 \mu\text{L}$) and concentration (overall unbagged mean = $10.68 \pm 0.21\%$ w/w) remains consistent throughout the day, and are within generalist nectar-feeding bird preferences, which may explain the abundance of Cape Weavers, despite floral morphological traits matching those of specialist nectar feeders. While many summer-flowering aloes are primarily insect- or sunbird-pollinated, Cape Weavers may be supplementing their diets with *A. reitzii* var. *reitzii* nectar, and potentially playing a crucial role in pollination.

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1. Introduction

Floral characteristics are often used to predict potential pollinators of a plant species, and create testable hypotheses for field experiments (Hargreaves et al., 2004; Ollerton et al., 2009). The most commonly utilised characteristics are flower shape and colour, flowering season, scent, and nectar properties (Faegri and van der Pijl, 1979; Dafni, 1992; Ollerton et al., 2009), which can vary within a genus. The genus *Aloe* L. (Asphodelaceae) comprises approximately 350 species in southern and eastern Africa, with a wide variety of growth forms and floral characteristics (Cousins and Witkowski, 2012; Van Wyk and Smith, 2014), predicting a diversity of primary pollinators (e.g. Hargreaves et al., 2008; Symes et al., 2008; Botes et al., 2009a, b; Arena et al., 2013). However, these predictions are not always accurate as visitors from multiple guilds are often attracted to the same flowers, despite some guilds not being predicted by floral characteristics (e.g. Hoffman, 1988; Botes et al., 2009a; De Merxem et al., 2009; Ollerton et al., 2009; Symes et al., 2009; Cousins et al., 2013).

Forty percent of South African aloes ($N = 158$ South African aloe species) flower in summer (December–February; Van Wyk and Smith, 2014). Summer-flowering aloes usually have short, tubular

flowers that are loosely packed on the raceme (Botes et al., 2009b; Wilson et al., 2009; Hargreaves et al., 2010; Van Wyk and Smith, 2014). Flowers are usually pale, but can be brightly coloured, and are sometimes borne on large, bold racemes (Van Wyk and Smith, 2014). Most of these aloes are visited by multiple guilds (i.e. both insects and specialist nectarivorous birds), and are primarily insect- and/or sunbird-pollinated, with generalist nectarivore birds having no significant effect on pollination (Botes et al., 2009b; Wilson et al., 2009; Hargreaves et al., 2010). Insects that pollinate these aloes include solitary bees (Megachillidae), sweat bees (Halictidae), membrane bees (Colletidae), honeybees, allodapine bees, and amegilla bees (Apidae) (Botes et al., 2009b; Wilson et al., 2009; Hargreaves et al., 2010). Although efficient pollinators, these insects can also act as nectar and pollen thieves, decreasing plant reproductive output (Hargreaves et al., 2010). Sunbirds, particularly the Malachite Sunbird (*Nectarinia famosa*), are primary pollinators of the summer-flowering *Aloe maculata*, and bees are pollen thieves (Hargreaves et al., 2010). Generalist nectarivores are not common visitors to, and/or pollinators of, summer-flowering aloes. In contrast, winter flowering aloe species tend to have different floral characteristics to summer flowering aloes (e.g. long, brightly coloured tubular flowers), and these aloes are usually pollinated by both specialist and/or generalist nectarivorous birds, and small, non-flying mammals, with insects usually playing a negligible role (Hoffman, 1988;

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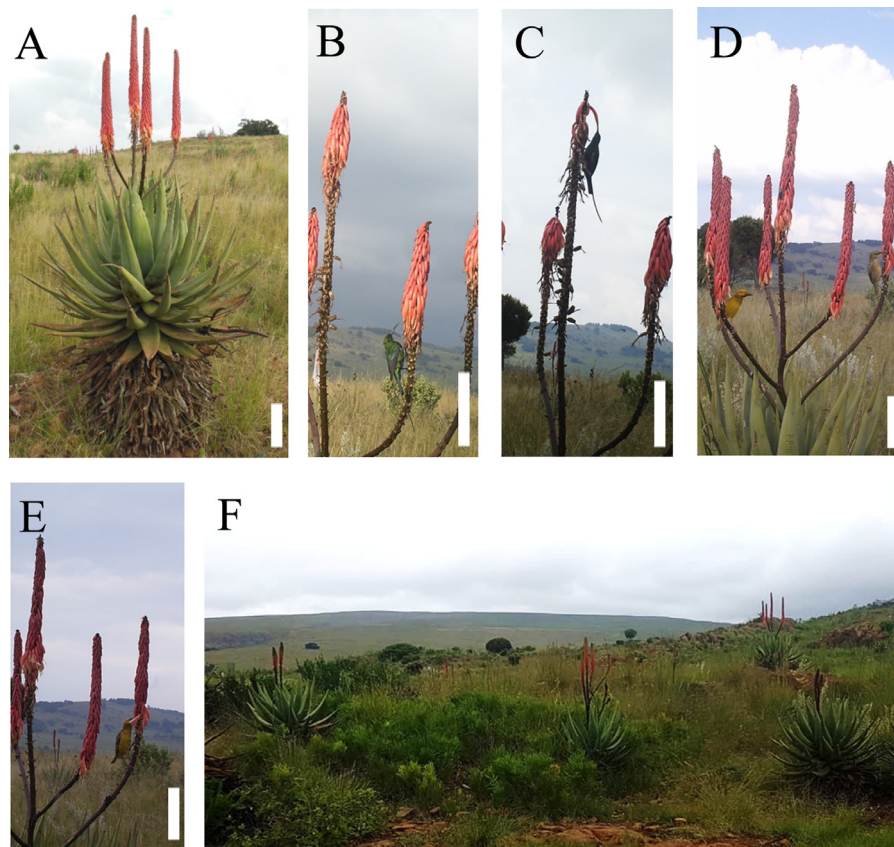


Fig. 1. A) A flowering *A. reitzii* var. *reitzii* plant; B) Male Malachite Sunbird (*Nectarinia famosa*) perched; C) Male Malachite Sunbird probing *A. reitzii* var. *reitzii* flower; D) Male and female Cape Weavers (*Ploceus capensis*) perched; E) Male Cape Weaver probing *Aloe reitzii* var. *reitzii* flower; F) *Aloe reitzii* var. *reitzii* in habitat on Klipbankspruit Farm, Tonteldoos, Mpumalanga. Scale bars: Photographs A–E = 10 cm. Photographs: Stephanie Payne.

Stokes and Yeaton, 1995; Johnson et al., 2006; Botes et al., 2008; Symes et al., 2008; Symes et al., 2009; Forbes et al., 2009; Hargreaves et al., 2012; Arena et al., 2013; Kuiper et al., 2015; Payne et al., 2016, 2019).

Aloe reitzii Reynolds var. *reitzii* (hereafter referred to as *Aloe reitzii*) is a summer-flowering aloe that displays a typical bird-pollination syndrome, with long, scarlet, tubular flowers (Fig. 1A; Faegri and van der Pijl, 1979; Symes, 2017). The flowers produce moderate volumes ($36 \pm 27 \mu\text{L}$) of concentrated nectar ($16.5 \pm 1.7\%$ w/w; Symes, 2017); these nectar characteristics are intermediate between that which suggest specialist nectarivore (sunbirds; volume: $10\text{--}30 \mu\text{L}$, concentration: $15\text{--}25\%$ w/w), and generalist nectarivore (volume: $40\text{--}100 \mu\text{L}$, concentration: $8\text{--}12\%$ w/w) preferences (Johnson and Nicolson, 2008; Symes, 2017). Indeed, Symes (2017) implicated both generalist and specialist nectarivorous birds, and insects as contributing to pollination. Three nectarivore bird species regularly visit *A. reitzii* – the generalist Cape Weaver (*Ploceus capensis*, 60% of visits), and the specialists Malachite Sunbird (27% of visits) and Greater Double-collared Sunbird (*Cinnyris afer*, 13% of visits; Symes, 2017). Honeybees (*Apis mellifera*), ants (*Camponotus* sp.), beetles (*Porphyronota* sp. and *Dischista* sp.) and grasshoppers (*Maura* sp.), were observed visiting the flowers and/or perching on the flowers or inflorescence stems (Symes, 2017). Since honeybees are primary pollinators of many summer-flowering aloes (Botes et al., 2009b; Wilson et al., 2009; Duffy et al., 2014), it is likely that they may play a role, along with the birds, in the pollination of *A. reitzii* (Symes, 2017).

The intermediate traits of nectar properties of *Aloe reitzii* reported by Symes (2017) are of interest, since most bird-pollination studies, especially those on aloes, are able to distinctly separate plants into generalist- and specialist-pollinated species based on floral morphology and nectar properties (e.g. Johnson et al., 2006; Botes et al., 2008,

Botes et al., 2009a; Johnson and Nicolson, 2008; Symes and Nicolson, 2008; Brown et al., 2009; Duffy and Johnson, 2011; Hargreaves et al., 2012; Cousins et al., 2013; Abrahamczyk, 2019). Similar to *A. reitzii*, visitation by both specialist and generalist nectar-feeding birds has been reported in *A. africana*, which also has nectar traits that are intermediate between specialist and generalist preferences (Botes et al., 2008; Johnson and Nicolson, 2008). It has been suggested that the floral traits are suited to specialist sunbirds, and the generalist birds are likely destroying the flowers as they feed on the nectar (Botes et al., 2008). However, Symes' (2017) observations were made over a very short period of the flowering season (~three days), and may not represent the full cohort of visitors to the aloes across the entire flowering season.

Therefore, this study recorded specialist and generalist nectar-feeding birds (the dominant visitors and most likely pollinators) visiting *Aloe reitzii* var. *reitzii* during the peak of the flowering season (February–March 2017). The following questions were addressed: 1) Which bird species visit, and dominate visitation to, the aloes during the peak of the flowering period? 2) Do nectar resources change throughout the day, and if so, do these changes reflect the preferences of the different nectar-feeding guilds at different times of the day? 3) Do the specialist- and generalist-nectar feeding birds partition their visits to the aloes, and therefore nectar resources, temporally?

2. Methods and materials

2.1. Study species and site

Aloe reitzii var. *reitzii* (Fig. 1A) is a stemless, Near Threatened aloe that is endemic to regions around Roosenekal, Belfast, and

Dullstroom, Mpumalanga, South Africa (Van Wyk and Smith, 2014; Mtshali et al., 2018). The green leaves are long (approx. 87 mm) and broad (up to 120 mm at the base), with reddish teeth along the margins, forming a large rosette (Van Wyk and Smith, 2014). The aloes flower during February and March, and can produce three racemes on average, but plants are known to produce between one and 10 racemes (Jepe, 1969; Van Wyk and Smith, 2014; Symes, 2017). The long, tubular flowers are red in bud, turning slightly yellow as they open and mature, from the base of the raceme upwards (Van Wyk and Smith, 2014), making the inflorescence very conspicuous in its environment when flowering. The aloe is distinguished from other similar species (e.g. *A. aculeata*) by its distinctly curved, downward pointing flowers (Jepe, 1969; Van Wyk and Smith, 2014).

Aloe reitzii is abundant (>1000 plants; Landowner, pers. comm.) on Klipbankspruit Farm, approximately 30 km north-west of Dullstroom, Mpumalanga (~1930 m a.s.l.). The 900 ha farm is privately owned and is used for commercial beef farming and grass-baling, mainly of *Eragrostis* and *Digitaria* species (Landowner, pers. comm.). Cattle, donkeys, and sheep regularly graze through the sites where the aloes are predominantly found. The farm is situated in Sekhukhune Montane Grassland, which is comprised of various habitat types, such as hills, rocky slopes and open grasslands with clusters of trees and shrubs (Mucina et al., 2006; Fig. 1F). The region received 121 mm of rain during the peak of the flowering season (February 2017; South African Weather Service, 2018).

2.2. Visitor observations

Animal visitors to the aloes over approximately three weeks during the peak of the flowering season in 2017 were recorded by motion-sensitive camera traps (Bushnell HD Model No. 119,537 and Bushnell Natureview Model No. 119,740, China). Over the course of 23 days (11 February–05 March 2017), 33 flowering *Aloe reitzii* plants were observed. These aloes were randomly selected, but selections represented the different habitats found along the farm (i.e. rocky slopes, flat grassland, rocky grassland, and wooded, rocky outcrops). Camera traps on tripods (height:~1.5 m) were placed approximately one metre away from the aloe, facing southwards. Cameras were set to take two photographs when triggered by motion, at three-second intervals; memory cards (SanDisk 2GB, 4GB, or 16GB) and batteries were changed as required (every 1–2 days). Cameras were set for the entire sampling period, with the exception of two days (16 and 17 February) where strong winds and heavy rain caused all cameras to fall over. Anecdotal researcher observations of visitors to any flowering aloes, during field sampling, were also recorded.

All animals recorded on the aloes during daylight hours (06:00–18:59) were considered as visitors. The distinction of daylight hours resulted in two birds (one unidentified sunbird which visited at 05:56, and one Southern Fiscal (*Lanius collaris*) which visited at 19:04) being excluded from all analyses. An animal was recorded as a visitor if it touched the aloe in any way (i.e. probed flowers, perched on racemes and/or leaves, etc.). Although an animal touching the plant may not be a legitimate pollinator, any contact with the plant was classified as an action used to implicate the animal as a potential flower visitor (Payne et al., 2016). If a visitor was photographed in successive frames, either on the same raceme, or a different raceme of the same aloe, it was considered the same visitor.

Visitors that left an aloe and appeared to return could not be confirmed as either the same or different visitors, so observations recorded >30 s apart (unless it was clear that it was the same individual, e.g. aberrant feather positioning, position on the aloe remained the same, etc.) were recorded as independent and new visits. Visitation rates for both the generalist and specialist pollinating guilds were calculated for each hour in a 24-hour period, for the duration of the sampling period. Overall visitation rates, and the percentage contribution for each visiting species, and for each guild over the entire

sampling period were calculated. Since many of the bird visitors were not frequently recorded (see Table 1), and due to the large number of camera hours recorded over the sampling period (~3942 daylight h; ~7383 h in total), visitation rates (visits/plant/hour) were extremely small, often exceeding six decimal places. The authors and the landowners estimate that there are >1000 individual *Aloe reitzii* plants on the farm (the authors measured >600 individual plants in a 1.8 km wandering transect section of the farm, SLP, unpubl. data). Owing to this, and the large number of decimal places when calculated as visits/plant/hour, visitation rates were extrapolated to, and presented as, the mean number of visits/1000 plants/hour, to account for potential visitation to the entire *A. reitzii* population on the farm.

2.3. Nectar production

Nectar properties were measured during daylight on 01 March 2017. One day prior (28 February 2017), ten flowering aloes were randomly selected, each with a minimum of two flowering racemes. On each aloe, one raceme was labelled as “bagged” and covered with a fine organza mesh bag, to measure nectar availability, and one raceme was left uncovered and labelled as “unbagged”, to measure nectar standing crop. Temperature data loggers (Thermocron iButtons, Australia, correct to 0.5 °C) were placed on each sampled raceme. Every two hours, starting at 07:00, nectar was extracted using disposable haematocrit tubes (75 µL) from one flower per raceme ($N = 56$ bagged flowers; $N = 47$ unbagged flowers; sampling was destructive). Nectar volume was recorded, and nectar sugar concentration (% w/w) was measured using a handheld refractometer (Bellingham & Stanley Eclipse Refractometer, Model 45–81, Tunbridge Wells, UK). Fully open flowers with newly dehisced anthers, were sampled. The stigma was receptive, but was not yet exerted past the stamens; *Aloe* nectar is most abundant during this stage of floral development (Human and Nicolson, 2008; Symes and Nicolson, 2008). Since only one specific stage was sampled, some racemes were not sampled in some sampling sessions as a suitable flower was not available. Labels, iButtons, and bags were removed after the final sampling session at 17:00. Sampling was undertaken on a hot day with clear skies in the morning (minimum temperature = 16.6 °C (05:00); maximum temperature = 26.8 °C (12:00)); a heavy thunderstorm began at approximately 17:30.

2.4. Data analysis

Visitation rates for generalist and specialist nectar-feeding guilds, were modelled as count data, with radians time and guild, and their interaction as fixed predictor variables using a Generalised Linear Model (GLM) with Poisson distribution and a log-link function. Visitation rates for the most frequent species from each feeding guild (Generalist = Cape Weaver; Specialist = Malachite Sunbird) were modelled as count data, using a GLM with radians time and species, and their interaction as fixed predictor variables with a Poisson distribution and log-link function. To account for hours of sampling effort for each aloe, an offset of number of camera hours that each aloe was recorded for was included in both visitation rate GLMs. Only daylight hours (06:00–18:59), were included in visitation rate analyses.

Activity level estimates – a measure of the proportion of the day that the visitors are active – were calculated for generalist and specialist nectar-feeding guilds, and for Cape Weavers and Malachite Sunbirds with 10,000 bootstrap samples, and Kernel Density Functions to show activity level over the daylight period were plotted, using the R package ‘activity’ (Rowcliffe et al., 2014; Rowcliffe, 2019). Activity level estimates were truncated between sunrise (~05:49) and sunset (~18:35) to account for time periods where diurnal avian visitors were not expected to be active (i.e. night-time hours excluded; Rowcliffe, 2019). Activity level estimates were compared

Table 1

Percentage contribution to total visitation and mean visitation rates (visits/hour/1000 plants; mean \pm S.E) of all generalist and specialist nectarivorous bird species visiting *Aloe reitzii* var. *reitzii* plants ($N = 33$ plants) during daylight (06:00 – 18:59), recorded by camera traps during three weeks of the peak of the February–March 2017 flowering season. Percentage contributions are calculated as percentage of the total number of visits by that species' guild, with contributions of the most regular visitor in bold text. Each species' activity was noted, as "feeding only", "perching only", or "both". "Perching only" includes visitors that were perching on leaves and/or inflorescences. The percentage of probing visits by each species are also presented (i.e. proportion of visits by that species where the birds were recorded probing flowers). References are provided for known *Aloe* nectar feeding birds and/or pollinators in Southern Africa. Bird taxonomy follows Hockey et al. (2005).

Species	Contribution (%); Visitation Rate (visits/hour/1000 plants)	Activity; Probing visits (%)	Known <i>Aloe</i> nectar feeder/pollinator (References)
GENERALIST NECTAR FEEDERS			
LANIIDAE			
Southern Fiscal	2.3	Perching only	Yes
<i>Lanius collaris</i>	0.93 \pm 0.63	0	7
MALACONOTIDAE			
Bokmakierie	0.6	Perching only	No
<i>Telophorus zeylanus</i>	0.60 \pm 0.60	0	–
PLOCEIDAE			
Cape Weaver	88.4	Both	Yes
<i>Ploceus capensis</i>	36.55 \pm 12.68	55.6	2,3,6,7,8,11,16
PYCNOTIDAE			
Dark-capped Bulbul	5.2	Both	Yes
<i>Pycnonotus tricolor</i>	2.94 \pm 1.56	44.5	2,4,13,14,17,18, 20
STURNIDAE			
Pied Starling	0.6	Perching only	Yes
<i>Spreo bicolor</i>	1.04 \pm 1.04	0	2,16
UNKNOWN	3.5	Both	–
Unknown Generalist Sp.	2.91 \pm 2.15	16.7	–
Total Number of Generalist Visitors	173	52.0	–
Total Generalist Visitation Rate	45.00 \pm 13.75	–	–
SPECIALIST NECTAR FEEDERS			
NECTARINIIDAE			
Amethyst Sunbird	1.0	Perching only	Yes
<i>Chalcomitra amethystina</i>	0.40 \pm 0.40	0	1, 3,5,9,10,12,14,18, 19, 20
Greater Double-collared Sunbird	4.0	Feeding only	Yes
<i>Cinnyris afer</i>	1.69 \pm 0.93	100	1, 4,5,16
Malachite Sunbird	90.6	Both	Yes
<i>Nectarinia famosa</i>	44.07 \pm 15.07	67.8	1,5, 8,10,11, 15,16
PROMEROPIDAE			
Gurney's Sugarbird	0.5	Feeding only	Yes
<i>Promerops gurneyi</i>	0.13 \pm 0.13	100	1
UNKNOWN	4.0	Both	–
Unknown Sunbird Sp.	4.15 \pm 2.72	62.5	–
Total Number of Specialist Visitors	202	68.3	–
Total Specialist Visitation Rate	50.57 \pm 17.38	–	–

References: ¹Skead, 1967.

²Oatley and Skead, 1972.

³Hoffman, 1988.

⁴Johnson et al., 2006.

⁵Botes et al., 2008.

⁶Symes and Nicolson, 2008.

⁷Symes et al., 2008.

⁸Forbes et al., 2009.

⁹Wilson et al., 2009.

¹⁰Hargreaves et al., 2010.

¹¹Symes, 2010.

¹²Duffy and Johnson, 2011.

¹³Hargreaves et al., 2012.

¹⁴Arena et al., 2013.

¹⁵Cousins et al., 2013.

¹⁶Kuiper et al., 2015.

¹⁷Payne et al., 2016.

¹⁸Patrick et al., 2018.

¹⁹Kremer-Köhne, 2018.

²⁰Diller et al., 2019.

between visiting guilds and Cape Weavers and Malachite Sunbirds with a Wald Test (Rowcliffe, 2019). Overlaps in visitation between the two nectar-feeding guilds, and the between Cape Weavers and Malachite Sunbirds were calculated and plotted, using the R package 'overlap' (Ridout and Linkie, 2009; Linkie and Ridout, 2011). Due to the large minimum sample size of recorded visits (> 75 minimum observations for both guilds and both species), the coefficient of

overlap "Dhat 4" ($\hat{\Delta}_4$) was used (Linkie and Ridout, 2011; Meredith and Ridout, 2018). A $\hat{\Delta}_4$ value of zero indicates no overlap in activity by the guilds/species of interest, while a $\hat{\Delta}_4$ value of one indicates complete overlap (Ridout and Linkie 2009; Linkie and Ridout 2011). Overlap confidence intervals were obtained from 10,000 smoothed bootstrap samples per overlap interaction (Ridout and Linkie, 2009; Linkie and Ridout, 2011; Meredith and Ridout, 2018).

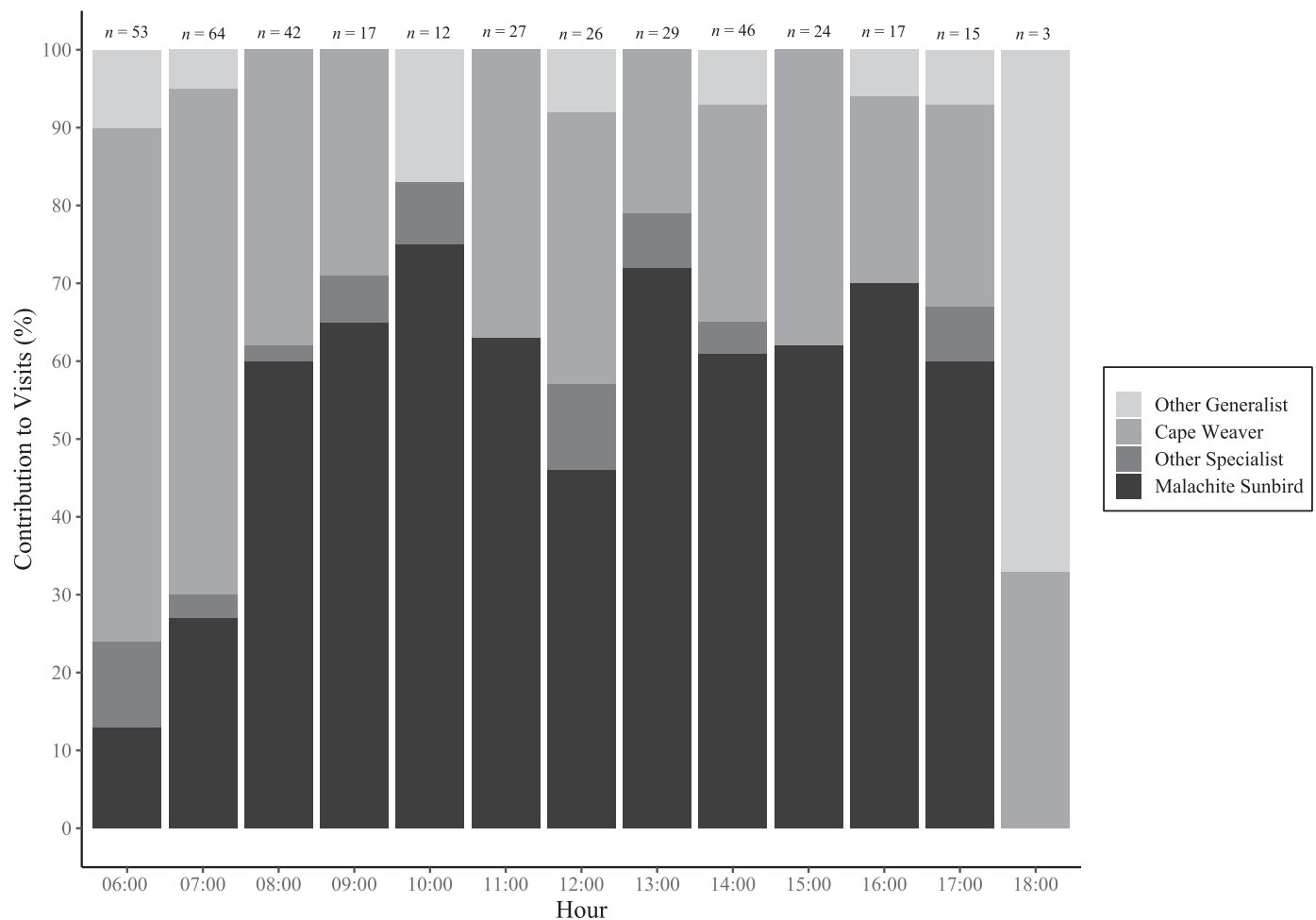


Fig. 2. Percentage contribution to visitation at each daylight hour (06:00 – 18:59) to *Aloe reitzii* var. *reitzii* plants by specialist nectarivorous birds and generalist (opportunistic) nectar-feeding birds, during three weeks of the peak of the February – March 2017 flowering season. Specialists are split into Malachite Sunbird (*Nectarinia famosa*), and other specialist species, while generalists are split into Cape Weaver (*Ploceus capensis*), and other generalist species. The total number of individual birds recorded for both guilds, at each hour, are presented above each stacked bar.

Both nectar volume and concentration data were not normally distributed (even after transformation), and hence were modelled using a Generalised Linear Mixed-effects Model (GLMM), with radians time and treatment, and their interaction, as predictor variables, and individual plant as a random effect. Nectar volume was modelled as a Poisson distribution. Nectar concentration values were recorded as a percentage, with the deficit (100% - recorded concentration) included in the model, which allowed the model to be tested with a binomial distribution and a logit-link function. Spearman rank correlations assessed whether nectar volume and concentration were correlated to temperature. All statistical analyses were performed in R (Version 4.0.1; R Core Team, 2020), GLMMs were run using the package “lme4” (Bates et al., 2015) and all graphics were produced using the R packages “ggplot2”, “extrafontdb” and “extrafont” (Chang, 2012, 2014; Wickham, 2016). Data are presented as mean \pm standard error.

3. Results

3.1. Visitor observations

A total of 375 individual birds representing nine bird species (five generalist, and four specialist nectar feeding species), were recorded visiting *Aloe reitzii* inflorescences over the sampling period (7383 total camera hours; Table 1). Fourteen individual birds could not be identified to species, due to poor light or the position of the bird on the inflorescence, and were broadly identified as generalists ($n =$ six

birds) or specialists ($n =$ eight birds), based on body and/or bill shape or size.

Visitation to the aloes was co-dominated by two bird species from different feeding guilds. Malachite Sunbirds (*Nectarinia famosa*) were the most common specialist nectar-feeding birds and overall visitors, accounting for 49% of all bird visits (Figs. 1B and 1C; Fig. 2; Table 1). Cape Weavers (*Ploceus capensis*) accounted for 41% of all bird visits, and were the most common generalist (opportunistic) nectar-feeding bird visitors (Figs. 1D and 1E; Fig. 2; Table 1). Forty percent of the sampled plants that received bird visits were visited by both species (along with other bird species), while 24% were visited only by Malachite Sunbirds, and 16% only by Cape Weavers (amongst other bird species).

Visitation to the aloes by both generalist and specialist guilds increased from 07:00, and began decreasing from 15:00 onwards (Figs. 2 and 3). Although Cape Weavers were the most frequent visitors between 06:00 and 08:00, the Malachite Sunbirds became more regular from 08:00 onwards, and were more consistent for the rest of the day (Figs. 2 and 3).

Three generalist individuals (Cape Weaver, Dark-capped Bulbul (*Pycnonotus tricolor*) and Southern Fiscal (*Lanius collaris*)) visited the aloes between 18:00 and 18:20. *Cisticola* sp. were observed perching on the racemes, but were not recorded on cameras (SLP, pers. obs.). A Gurney’s Sugarbird (*Promerops gurneyi*) was observed trying to feed on nectar, but was chased by a male Malachite Sunbird. The sugarbird was later recorded feeding on another aloe.

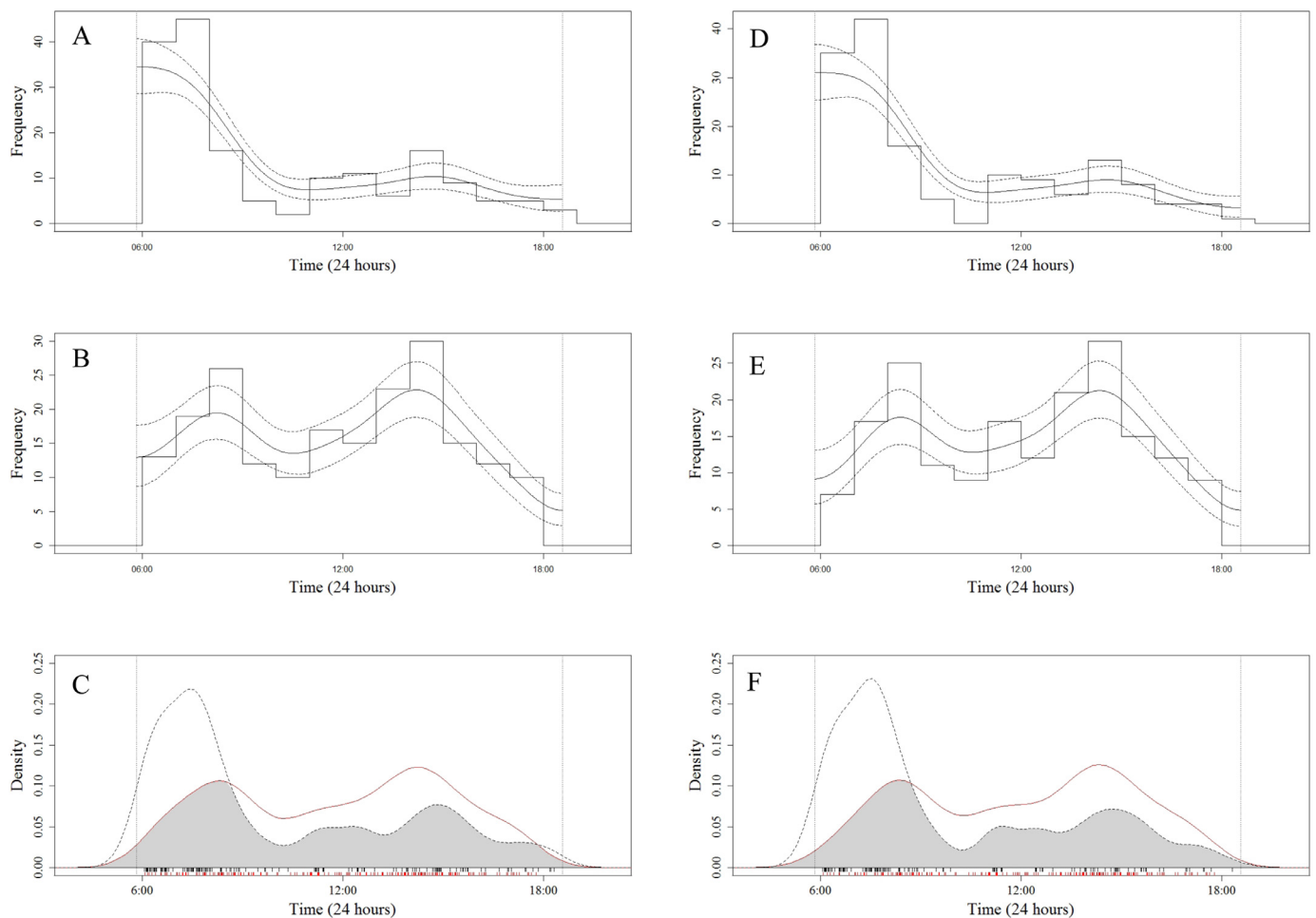


Fig. 3. A) Generalist nectar-feeding birds activity levels, B) Specialist nectar-feeding birds activity levels, C) Overlaps in visitation by Generalist nectar-feeding birds (dashed black line) and Specialist nectar-feeding birds (solid red line), D) Cape Weavers (*Ploceus capensis*) activity levels, and E) Malachite Sunbirds (*Nectarinia famosa*) activity levels, and F) Overlaps in visitation by Cape Weavers (dashed black line) and Malachite Sunbirds (solid red line). All graphs are based data recorded by camera trap observations of 33 *Aloe reitzii* var. *reitzii* plants during three weeks of the peak of the February – March 2017 flowering season. Activity level graphs are truncated between sunrise (~05:49) and sunset (~18:35) to account for periods of assumed inactivity (i.e. no nocturnal activity by birds). Solid black stepped lines are actual frequencies, while curved lines are smoothed, fitted circular kernel distributions (with 10 000 bootstraps). Vertical dashed lines represent sunrise and sunset. Overlaps in activity are represented by Kernel Density Estimate graphs. Shaded grey areas indicate periods of overlap in visitation, and individual visits are represented by small vertical lines along the x-axis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Honeybees (*Apis mellifera*, Hymenoptera: Apidae) were observed visiting flowers, removing nectar, and pollen. Koppie Foam Grasshoppers (*Dictyophorus spumans*) and Elegant Grasshoppers (*Zonocerus elegans*; both Orthoptera: Pyrgomorphidae) were recorded perching on racemes, sometimes moving between racemes and plants, but were not recorded feeding on nectar or pollen. Coleoptera (*Dischista* sp. and *Porphyronota* sp.; Scarabaeidae: Cetoniinae) were often perched on racemes, or burrowed between individual flowers, possibly feeding on flower material and/or piercing flowers to gain access to the nectar (James du G. Harrison, *pers. comm.*). Both grasshoppers and beetles are not likely to be performing any pollination function. Camera traps recorded hawkmoths, likely *Agrius* sp. (Nic Venter, Craig Peter, *pers. comm.*), visiting the aloes from 18:10, and continuing to regularly visit ($N = 148$ total records) throughout the night until sunrise. One Striped Hawkmoth (*Hyles livornica*) was recorded at one aloe during the day.

Generalist and specialist nectar-feeding bird visitation rates do not differ significantly (Guild; Table 2), but the significant interaction between guild visitation rates and time, indicates that visitation is separated temporally by guild (Table 2), with generalists dominating visitation in the early morning (Fig. 2). Overall, bird visitation rates decreased significantly over time throughout the day (Radians_Time;

Table 2), despite the specialists consistently visit the aloes from the mid-morning into the early evening (Fig. 2). The activity level estimates show a significant difference in the proportion of the day that the two feeding guilds are active ($W = 24.81$, $p < 0.001$), with generalists being very active for a shorter time period (activity level estimate = 0.39 ± 0.03 ; Fig. 3A), while specialists are active for a greater proportion of the day (activity level estimate = 0.69 ± 0.05 ; Fig. 3B). There was moderate amount of overlap in visitation times between generalists and specialists ($\Delta_4 = 0.69$, 95% C.I = 0.60 – 0.77), suggesting that while there is still some overlap in visitation, visitors from the two feeding guilds are partitioning visitation to the aloes temporally for a portion of the day (Fig. 3C).

In accordance with above, Malachite Sunbird and Cape Weaver visitation rates were not significantly different, with both species contributing equally to visitation (Species; Table 2). Overall visitation rates by these species decreased over time (Radians_Time), but the significant interaction between species and time indicate that visitation by these two species was temporally separated (Table 2), with Malachite Sunbirds dominating visitation from the late morning onwards. Activity level estimates are significantly different between species ($W = 21.78$, $p < 0.001$), suggesting that Cape Weavers are very active for a shorter portion of the day (activity level

Table 2

Results of statistical models for visitation rates and nectar properties. Parameter estimates (β), with standard errors (S.E.), significance of each factor and 95% Confidence Intervals (C.I.), are presented. Visitation rates for guilds and species were modelled as a General Linear Models (GLM), while nectar volume and concentration were modelled as Generalised Linear Mixed-Effect Models (GLMM). Significant p -values are highlighted in bold. (Guild(Generalist)) was the reference category for the guild factor in the Guild Comparison model, and (Species(Malachite Sunbird)) was the reference category for the species factor in the Species Comparison models respectively. In both nectar models, (Treatment(Bagged)) was the reference category for the treatment factor.

Predictor	$\beta \pm$ S.E.	p -Value	95% C.I.	
			2.5%	97.5%
<i>Guild Comparison: Generalist vs Specialist Visitation Rates</i>				
Intercept	-1.92 \pm 0.08	<0.001	-2.07	-1.77
Guild(Specialist)	0.06 \pm 0.11	0.58	-0.15	0.27
Radians_Time	0.25 \pm 0.11	0.03	0.03	0.47
Guild(Specialist):Radians_Time	-0.76 \pm 0.16	< 0.001	-1.07	-0.45
<i>Species Comparison: Malachite Sunbird vs Cape Weaver Visitation Rates</i>				
Intercept	-1.97 \pm 0.08	< 0.001	-2.13	-1.81
Species(Weaver)	-0.06 \pm 0.12	0.59	-0.29	0.16
Radians_Time	-0.56 \pm 0.12	< 0.001	-0.79	-0.34
Species(Weaver):Radians_Time	0.79 \pm 0.17	< 0.001	-0.47	1.12
<i>Nectar Volume</i>				
Fixed Effects				
Intercept	4.34 \pm 0.12	< 0.001	4.10	4.58
Treatment(Unbagged)	-0.56 \pm 0.17	0.001	-0.91	-0.21
Radians_Time	-0.03 \pm 0.02	0.21	-0.07	0.01
Treatment(Unbagged): Radians_Time	-0.25 \pm 0.04	< 0.001	-0.32	-0.18
Random Effect: Plant ID: Variance = 0.146, Standard Deviation = 0.382				
<i>Nectar Concentration</i>				
Fixed Effects				
Intercept	-2.14 \pm -0.04	< 0.001	-2.23	0.08
Treatment(Unbagged)	0.02 \pm 0.07	0.79	-0.11	0.14
Radians_Time	0.01 \pm 0.06	0.81	-0.10	0.13
Treatment(Unbagged): Radians_Time	-0.09 \pm 0.09	0.33	-0.26	0.09
Random Effect: Plant ID: Variance = 0 Standard Deviation = 0.				

estimate = 0.39 ± 0.03 ; Fig. 3D) while Malachite Sunbirds are active for a greater proportion of the day, spreading their visits out over the daylight hours (activity level estimate = 0.67 ± 0.05 ; Fig. 3E). There is only a moderate amount of overlap between the two species ($\Delta_4 = 0.66$, 95% C.I. = 0.56 – 0.75), indicating that the two species are partitioning visitation to the aloes temporally for part of the day (Fig. 3F).

3.2. Nectar production

Nectar is produced continually throughout daylight hours (Fig. 4A). A significant interaction between treatment and time suggest that nectar volumes for bagged and unbagged flowers were equally affected by time, although volume in both treatments did not appear to change significantly over daylight hours (Radians_Time; Table 2). Nectar volumes in unbagged plants were significantly lower than bagged plants (Treatment; Table 2). Mean bagged nectar volumes peaked at 07:00 ($100 \pm 20.3 \mu\text{L}$, $n = 10$ flowers), and were lowest at 17:00 ($65.9 \pm 11.9 \mu\text{L}$, $n = 10$ flowers). Mean unbagged nectar volumes were highest at 11:00 ($70.1 \pm 16.7 \mu\text{L}$; $n = 8$ flowers) and lowest at 15:00 ($36.6 \pm 5.6 \mu\text{L}$; $n = 8$ flowers).

Nectar concentration did not differ between treatments, nor did it change over time (Treatment; Radians_Time; Table 2; Fig. 4B). The interaction between nectar concentration and time had no significant effect on nectar concentration, suggesting that nectar concentrations remained similar throughout the day for both treatments (Table 2). Mean bagged nectar concentrations were highest at 15:00

($11.3 \pm 0.3\%$ w/w; $n = 6$ flowers), and lowest at 07:00 ($9.7 \pm 0.6\%$ w/w; $n = 10$ flowers). Mean unbagged nectar concentrations peaked at 11:00 ($11.5 \pm 0.5\%$ w/w; $n = 8$ flowers), and the lowest concentrations measured at 07:00 ($9.1 \pm 0.6\%$ w/w).

Temperature and nectar volume were not correlated for either the bagged or unbagged treatments (Bagged: $R_S = -0.10$, $P = 0.48$; Unbagged: $R_S = -0.04$, $P = 0.81$). Unbagged nectar concentration was not correlated with temperature ($R_S = 0.26$, $P = 0.08$), while bagged nectar concentration was weakly, positively correlated with temperature ($R_S = 0.31$, $P = 0.02$). At lower temperatures, when not directly exposed to environmental elements, nectar may be more concentrated (Fig. 4B).

4. Discussion

4.1. Role and partitioning of specialist and generalist avian visitors

Aloe reitzii displays floral characteristics typical of an ornithophilous (bird) pollination syndrome, with long (~50 mm; Van Wyk and Smith, 2014), tubular red flowers that produce large amounts of dilute nectar throughout the day (Faegri and van der Pijl, 1979; Johnson and Nicolson, 2008). This study found that nectar properties were mostly in the preferred range for generalist pollinators (Johnson and Nicolson, 2008), while Symes (2017) found that the nectar properties were more suited to specialist pollinators, although volumes and concentrations did extend into the preferred range for generalist pollinators. This broad range of nectar properties may explain the similar visitation rates, and co-dominance, of specialist sunbirds and generalist weavers. While this study recorded the same flower visitors as Symes (2017), with the addition of six more species (Table 1), the proportion of visits by the dominant species were opposite. The Malachite Sunbird was the most frequent visitor (49% of all bird visits), and visited more frequently than previously recorded in Symes (2017), where it only comprised 27% of all bird visits, while Cape Weaver visitation was less than previously recorded (this study: 41% of all bird visits; Symes 2017: 60% of all bird visits). Although nectar properties do not change to suit one guild or the other during the course of the day, these species appear to partition the nectar resource temporally, with the Cape Weaver dominating early morning visitation. The potentially shared role of both the Cape Weaver and the Malachite Sunbird in the pollination of this aloe is reinforced (Symes, 2017), although exclusion experiments, assessments of the pollen-loads of the individual species, and/or pollen tracking-experiments with fluorescent dyes, are required to quantify the individual contributions of each of these species to effective cross-pollination.

The Cape Weaver is a regular visitor to many winter-flowering aloes, including *Aloe ferox*, *A. candelabrum*, *A. arborescens*, *A. spectabilis* and *A. marlothii* (Oatley and Skead, 1972; Hoffman, 1988; Stokes and Yeaton, 1995; Symes and Nicolson, 2008; Symes et al., 2008; Forbes et al., 2009; Kuiper et al., 2015). Although insectivorous, most weavers are opportunistic nectar-feeders and have been described by Oatley (1964) as “addicted probers”, since they regularly feed on the abundant nectar of many other flowering species, such as *Erythrina* and *Schotia*, amongst others (Oatley, 1964; Jacot Guillarmod et al., 1979; Symes and Yoganand, 2013; Craig, 2014); the Cape Weaver is likely the same, feeding on the abundance of *Aloe* nectar available during peak flowering (Kuiper et al., 2015). Malachite Sunbirds are commonly territorial (Skead, 1967) and are known to chase other birds from food and breeding resources (Hargreaves et al., 2004; Geerts and Pauw, 2009a). There may be competition between the species for nectar resources, as suggested by the high proportion of plants that were visited by the Malachite Sunbird only, compared to the Cape Weaver. This could also explain the temporal partitioning between the two species and more regular visitation by the Malachite Sunbird, as well as absence of other sunbird species and sugarbirds (Geerts and Pauw, 2009a).

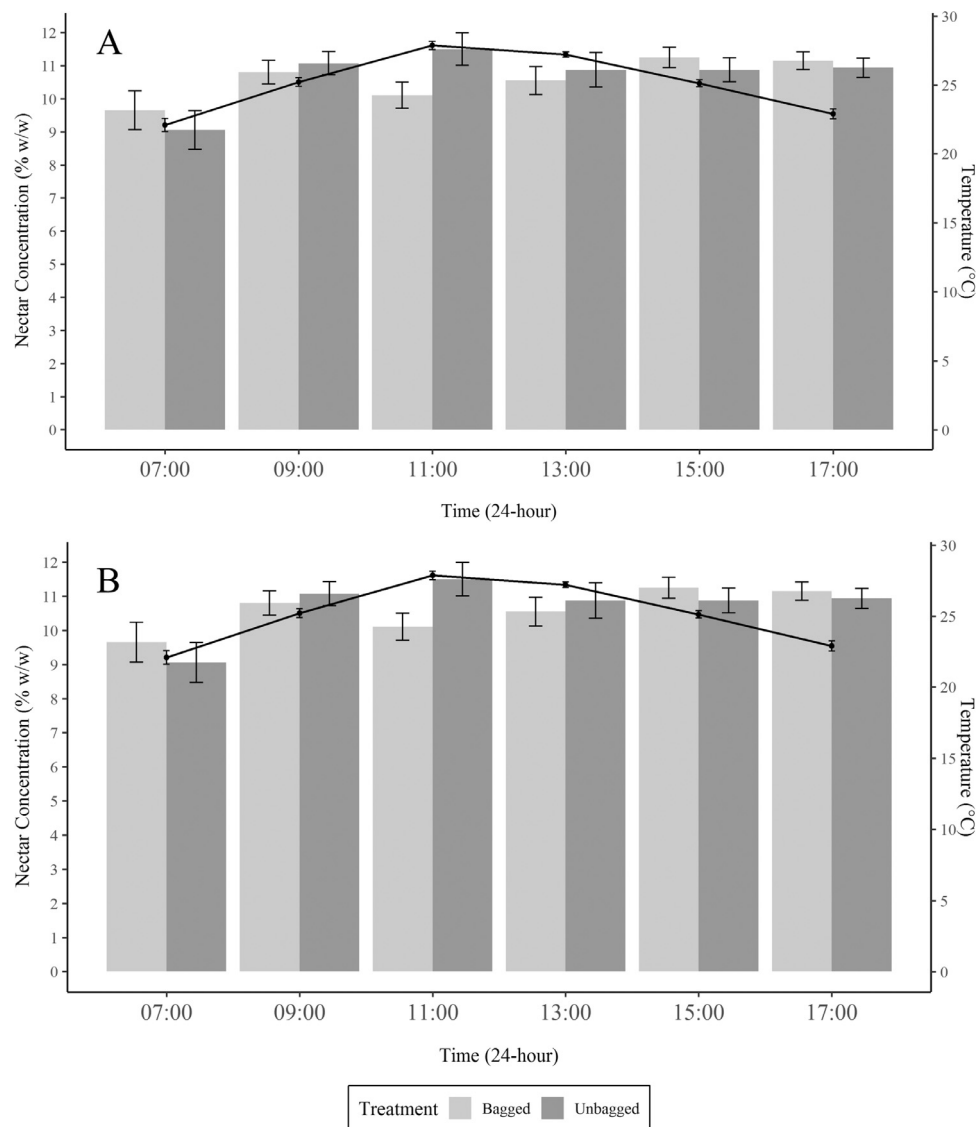


Fig. 4. A) *Aloe reitzii* var. *reitzii* nectar volumes (μL ; mean \pm S.E.) and B) concentrations (% w/w; mean \pm S.E.) of bagged and unbagged plants ($n \leq 10$ flowers per time period per treatment; $N = 10$ plants per treatment), measured at two-hour intervals during daylight hours. Mean temperature ($^{\circ}\text{C}$; mean \pm S.E.) is represented by the solid black line.

Floral length and curvature are often correlated with pollinating bird bill morphology (e.g. Cronk and Ojeda, 2008; Geerts and Pauw, 2009a; Van der Niet et al., 2014; Maglianesi et al., 2015; Johnson et al., 2020). Costa Rican hummingbirds have been shown to select plants with floral traits that match their own bill morphology (i.e. birds with long, curved bills preferentially select long, curved, tubular flowers; Maglianesi et al., 2015). This has also been shown in the Cape provinces of South Africa, where many plants are pollinated by birds whose bill morphology matches floral morphology (e.g. Geerts and Pauw, 2009a, Van der Niet et al., 2014). These plants are suggested to have evolved a “Malachite Sunbird Pollination Syndrome”, where floral tubes have elongated and become exclusively pollinated by Malachite Sunbirds (Geerts and Pauw, 2009a). Such flowers usually have a floral tube length ranging from 35 to 58 mm, which excludes shorter-billed birds from legitimately accessing the nectar and/or nectaries at the base of the floral tube (Geerts and Pauw, 2009a). Malachite Sunbird bill lengths range from 29 mm (female) to 32 mm (male; Dowsett-Lemaire, 1989), and up to 51 mm with the tongue extended (Geerts and Pauw, 2009a). *Aloe reitzii* floral tubes are approximately 50 mm long (Van Wyk and Smith, 2014), and Malachite Sunbirds can no doubt easily access and drink the

nectar. Floral length, causing the exclusion of smaller sunbird species, may be resulting in the aloe morphology tending towards a long-billed bird specialised pollination syndrome, such as the Malachite Sunbird Syndrome (Geerts and Pauw, 2009a). Although *A. reitzii* pollen was not clearly visible on the feathers of the Malachite Sunbirds (SLP, *pers. obs.*), these birds might be picking up small amounts of pollen on their long, narrow bills (Geerts and Pauw, 2009b), since narrow corolla tubes can facilitate the transfer of pollen onto a bird’s bill as it probes the flower (Hargreaves et al., 2019). Conversely, Cape Weavers forced their short bills into the flowers (from the mouth of the flower) to access nectar, and their bills and foreheads became covered in pollen (SLP, *pers. obs.*). Although this behaviour might destroy the corolla (e.g. Geerts and Pauw, 2009b), as long the pistil remains intact (Faegri and van der Pijl, 1979), weavers may be more effective at transferring larger amounts of *Aloe* pollen than Malachite Sunbirds (Kuiper et al., 2015). This reinforces the need for pollen-load measurements of these two bird species.

Aloe ferox, a winter-flowering aloe, is predominantly visited by Malachite Sunbirds and *Ploceus* weavers, both of which track the seasonal nectar resources and respond to the increase in nectar availability (Kuiper et al., 2015). Bird densities often increase in winter

months when large aloes are in flower (Symes et al., 2008; Forbes et al., 2009; Kuiper et al., 2015), with sunbirds, in particular, migrating in response to resource availability (Craig and Hulley, 1994). The Malachite Sunbird is a “tourist”, following a regular route between resources, but can also act as a “shopper”, opportunistically feeding at seasonally available, resource rich sites (Craig and Hulley, 1994; Symes et al., 2001). These mixed strategies of the Malachite Sunbird movements largely depend on the seasonality and proportion of plants flowering in a population (Symes et al., 2001). A greater proportion of *Aloe reitzii* plants were flowering in 2017 (29% of 533 sampled plants; SLP, unpubl. data), compared to 2014 (18.9% of 726 sampled plants; Symes, 2017), and this increase in resource availability across the entire sub-population (>1000 plants; Landowner, pers. comm.) might explain the considerable increase in Malachite Sunbird visitation between years.

Cape White-eye (*Zosterops capensis*), Fork-tailed Drongo (*Dicrurus adsimilis*), Cape Rock-Thrush (*Monticola rupestris*), Red-winged Starling (*Onychognathus morio*) and Southern Masked Weaver (*Ploceus velatus*) are well-known *Aloe* visitors, often tracking the increased production of nectar during peak flowering (Oatley, 1964; Skead, 1967; Johnson et al., 2006; Symes et al., 2008; Botes et al., 2008; Botes et al., 2009a; Forbes et al., 2009; Symes et al., 2009; Hargreaves et al., 2012; Arena et al., 2013; Kuiper et al., 2015; Payne et al., 2016, 2019; Patrick et al., 2018). These species were not seen on the farm or feeding at these aloes, but have been observed in the region during January–April (South African Bird Atlas Project 2, 2018). Their absence is of interest, particularly in the case of the Cape White-eye. However, these species are primarily insectivores, and mostly feed on *Aloe* nectar in winter to supplement their diets when insects are less active (Symes et al., 2008). Thus, nectar may be less important in summer, and the birds do not rely on summer-flowering aloes as much as winter-flowering species. Their absence may also be due to the fragmentation of the aloe habitat for farming, or they are being chased away by the territorial Malachite Sunbirds (Skead, 1967). Amethyst Sunbirds (*Chalcomitra amethystina*), have been seen feeding on *Aloe reitzii* nectar (Landowner, pers. comm.), but were not recorded as regular visitors in this study.

4.2. Diurnal and nocturnal insect visitors

Insects, particularly honeybees and solitary bees, are the primary pollinators of many summer-flowering aloes (Botes et al., 2009a, b; Wilson et al., 2009; Duffy et al., 2014), with birds playing a minor role in the pollination of these species (Botes et al., 2009a). The flowers of these aloes tend to have shorter corollas (<20 mm; Hargreaves et al., 2012), and produce substantially less nectar than bird-pollinated aloes (e.g. $0.097 \pm 0.10 \mu\text{L}$ in *Aloe inconspicua*, Hargreaves et al., 2008). Although their contribution was not quantified, honeybees, with full pollen baskets, were regularly recorded on *A. reitzii* flowers, and were often seen on the filaments of the stamens, which protrude past the mouth of the flower, presumably drinking nectar that was dripping out of the flowers (SLP, pers. obs.). Bees are known pollen thieves in the sunbird-pollinated, summer-flowering *A. maculata*, negatively affecting fecundity (Hargreaves et al., 2010); a similar scenario may be occurring in *A. reitzii*, where bees are removing nectar and pollen, but not successfully transferring pollen between flowers.

Symes (2017) recorded moths visiting the aloes at night, but only for approximately two hours early in the evening. In this study, hawkmoths were recorded visiting the aloes throughout the night and into the early hours of the morning. Moth-pollinated flowers are usually white, and heavily scented with nocturnal anthesis (Baker, 1961; Faegri and van der Pijl, 1979). *Aloe reitzii* is a scentless aloe, and although flowers do not close at night, anthesis does become slower at night, as with other *Aloe* species (Symes et al., 2008; Payne et al., 2016). Although hawkmoths are important

pollinators of long-tubed flowers in Africa (e.g. Johnson and Raguso, 2016), moth pollination is not recorded in *Aloe*. However, the sheer abundance of moths recorded visiting these aloes is of interest, and may suggest either a role in pollination, or nectar thieving as they drink nectar droplets, highlighting the need for nocturnal exclusions (e.g. Payne et al., 2016).

4.3. Small mammal visitors

Anecdotal reports describe sengi (*Elephantulus* sp.) visiting the aloes on a ridge in the farm (Landowner, pers. comm.), but camera trapping on the ridge ($n = 4$ plants, ~824 h), did not record any small mammal visitors. Symes (2017) did not record any small-mammals either, despite setting cameras up to record them. *Aloe peglerae*, a winter-flowering aloe endemic to the Magaliesberg Mountain Range, is successfully pollinated by the Namaqua Rock Mouse (*Micalamys namaquensis*) and sengi at night, along with its primary bird pollinator, the diurnal Cape Rock-thrush (*Monticola rupestris*; Arena et al., 2013; Payne et al., 2016). Food resources are often scarce in winter, and the small mammals may be relying on the aloe nectar as an energy source (Wiens et al., 1983; Johnson, 2004; Payne et al., 2016, 2019), whereas in summer, food resources are more readily available (particularly insects for the insectivorous sengi), and small mammals may not be as reliant on nectar. Also, *A. peglerae* is a smaller aloe that is closer to the ground, allowing for more ground cover, than *A. reitzii* (*A. peglerae* flowering height: ~40 cm; *A. reitzii* flowering height: ~1.5 m; Jeppe, 1969), and accessing the more exposed *A. reitzii* nectar may pose a greater predation risk (e.g. Jensen et al., 2003).

Conclusion

The abundance of diurnal birds, along with diurnal and nocturnal insects suggests that multiple guilds are attracted to, and rely on, *Aloe reitzii* nectar. This aloe produces nectar constantly throughout the day, and this is likely the major attractant for visitors, as bird visitation trends appear to track nectar production. Specialist and generalist nectar-feeding birds co-dominate visitation to *A. reitzii*, but partition the nectar resource temporally. Within each of these visiting guilds, there is a “dominant” visitor that accounts for the majority of visitation events. The relatively equal abundance of two bird species from two different guilds visiting *A. reitzii* is unusual, as many summer-flowering aloes are primarily insect- and/or sunbird-pollinated. Many studies of bird-pollinated plants are able to draw distinct conclusions about whether the plant is generalist or specialist pollinated (e.g. Johnson et al., 2006; Johnson and Nicolson, 2008; Symes and Nicolson, 2008; Symes et al., 2008; Botes et al., 2008; Botes et al., 2009a; Brown et al., 2009; Wilson et al., 2009; Arena et al., 2013; Abrahamczyk, 2019), based on floral traits, nectar properties, and/or visitation to the plant which is dominated by one specific feeding guild. This is not so clear-cut in *A. reitzii*. While the aloe has floral traits suggestive of long-billed bird pollination (long, narrow, curved, floral tubes; Geerts and Pauw, 2009a; Van der Niet et al., 2014; Maglianesi et al., 2015) the nectar properties are indicative of generalist bird pollination (Johnson and Nicolson, 2008). This highlights the need for detailed breeding system and pollination studies of this *Aloe* species and, more broadly, the work that is still required to understand the different feeding guilds within the bird pollination syndrome.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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