Appearances can be deceiving: Pollination in two sympatric winter-flowering *Aloe* species

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Abstract

Aloe marlothii and *A. greatheadii* var. *davyana* are two sympatric winter-flowering succulents that occur in the summer rainfall regions of northern and north-eastern South Africa. Both have flower characteristics that are strongly suggestive of bird pollination, although their nectar differs in volume and concentration. We conducted pollinator exclusion experiments to determine the importance of birds and insects as pollinators of these *Aloe* species. For both species fruit set and the number of seeds per fruit were higher in control treatments (all pollinators) and lower in treatments that excluded all pollinators. The contribution of insect pollinators to fruit set in *A. marlothii* was low (3–4%), like that of no pollinators (0–2%) whilst that of all pollinators (14–19%) was significantly higher, suggesting that generalist avian pollinators, which visited flowers in large numbers, are the most important pollinators. In *A. greatheadii* var. *davyana* fruit set in the absence of pollinators was also very low (2–6%), while the contribution to fruit set by insects (36–51%) was similar to that of all pollinators (55–55%), confirming the importance of honeybees to pollination. Clear understanding of both flower and nectar characteristics, and observations of flower visitors, are therefore required before an accurate prediction of pollinator type can be made.
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Keywords: Co-flowering; *Greatheadii*; *Marlothii*; Nectarivore; Ornithophily; Sunbird

1. Introduction

The reliability of pollination syndromes for predicting pollinator types has recently been questioned and in many plant species multiple visitors may be involved in pollination (Waser et al., 1996; Ollerton, 1998; Johnson and Steiner, 2000). Plants that are apparently adapted for pollination by birds are frequently also visited by insects, although the latter may be inefficient pollinators. In Australia, introduced honeybees *Apis mellifera*, which are ineffective pollinators of many native plants, displace effective indigenous pollinators (Paton, 1993; Vaughton, 1996). In South Africa, *Protea roupelliae* has flower characteristics reflecting specialisation for bird pollination and is pollinated by malachite

sunbirds *Nectarinia famosa*, but also attracts beetles and honeybees that are less efficient pollinators (Hargreaves et al., 2004). Flower characteristics of many *Aloe* species, such as bright orange–red perianths with exserted anthers and stamens, and copious amounts of dilute nectar at the base of the flower, strongly suggest a bird pollination syndrome (Faegri and Van der Pijl, 1979; Proctor et al., 1996). Without experimental evidence, Tribe and Johannsmeier (1996) considered both sunbirds and honeybees to be the major pollinators of three species of tree aloe (*A. dichotoma*, *A. pillansii* and *A. ramosissima*) and, because honeybees visited *A. ferox* flowers in greater abundance than birds, they were suspected by Skead (1967) to be more important pollinators. Hoffman (1988) also predicted honeybees to be important pollinators of *A. ferox* but the importance of experimental studies was highlighted by Stokes and Yeaton (1995) who found that honeybees made very little contribution as pollinators in *A. candelabrum* (later merged with *A. ferox*). Only recently have the true pollinators of some *Aloe* species been confirmed (Johnson et al., 2006; Hargreaves et al., 2008;

Botes et al., 2009; Wilson et al., 2009). Visitation of a plant species by members of a certain pollination guild does not necessarily mean they are the most important pollinators. Positive confirmation of the true pollinators of the numerous *Aloe* species requires field experiments and observations.

Typical bird pollination characters are evident in two winter-flowering *Aloe* species that have closely sympatric distributions in the northern and north-eastern summer rainfall regions of South Africa (Reynolds, 1969; Glen and Hardy, 2000; Van Wyk and Smith, 2005; Table 1). Both species frequently grow in large stands of hundreds to thousands of plants and flower in profusion during dry winter months between May and September (Van Wyk and Smith, 2005). *Aloe marlothii* is a single stemmed aloe that reaches up to 6 m in height and is abundant on rocky north-facing slopes (Reynolds, 1969; Glen and Hardy, 2000; Van Wyk and Smith, 2005; Fig. 1). Its bright orange to red tubular flowers, on conspicuous inflorescences, produce large quantities (250 μl/ flower) of dilute nectar (12%) that attracts a variety of nectar-feeding birds throughout the species' range (Oatley, 1964; Oatley and Skead, 1972; Symes et al., 2008; Symes and Nicolson, 2008). *Aloe greatheadii* var. *davyana*, a smaller and less conspicuous spotted aloe, producing salmon pink to red flowers, grows well in rocky terrain and grassy plains (Glen and Hardy, 2000; Smith and Crouch, 2001; Fig. 1). The small robust plants, whose inflorescences seldom exceed 1.0 m in height, occur most densely in overgrazed areas (Clark, 1992). This is an important plant for migratory beekeepers, who move their hives to the aloe fields to utilise the strong nectar and pollen flow to build up their colonies and obtain a substantial honey crop (Williams, 2002). In contrast to those of *A. marlothii*, *A. greatheadii* var. *davyana* flowers produce less nectar (33 μl/flower) of a higher concentration (21%) (Human, 2006; Human and Nicolson, 2008).

Nectar properties are associated with specificity in bird pollination systems: flowers producing nectars of high volume (40–100 μl/flower) and low concentration (8–12% w/w) attract generalist bird pollinators, whilst those producing nectars of low volume (10–30 μl/flower) and higher concentration (15–25% w/w) attract specialist nectarivores such as hummingbirds and sunbirds (Johnson and Nicolson, 2008). We therefore hypothesized that, in these two aloes, bird pollinator type would be defined by nectar characteristics. We expected flowers of *A. marlothii*, with nectar of relatively high volume and low concentration, to be pollinated by generalist avian pollinators and those of *A. greatheadii* var. *davyana*, with nectar of lower volume and higher concentration, to be pollinated by specialist avian pollinators (i.e. sunbirds).

2. Materials and methods

2.1. Study site

Pollinator exclusion experiments were conducted on *A. greatheadii* var. *davyana* during 2003 and 2004 at Roodeplaat Nature Reserve (size 795 ha, 30 km east of Pretoria), and on *A. marlothii* during 2006 and 2007 at Suikerbosrand Nature Reserve (19 780 ha, 60 km south-east of Johannesburg). The study sites fall within summer rainfall areas, and the winter flowering seasons of these aloes are characterised by pronounced daily temperature changes with warm days and cold, sometimes frosty, nights.

At Roodeplaat honeybees *Apis mellifera scutellata* were abundant visitors to *A. greatheadii* var. *davyana* flowers in 2003. During 2004, six bee hives were placed in the reserve for other experiments, replicating conditions where beekeepers move their hives to the aloe fields.

2.2. Exclusion experiments and compatibility

In two successive years three treatments were applied to racemes on 20 different plants of each *Aloe* species as follows: i) control treatment — unrestricted access by all floral visitors, raceme marked with identifying flagging tape; ii) insects only — cage placed around whole raceme, constructed of a rigid plastic mesh (see Johnson et al., 2006) for *A. marlothii* and wire mesh for *A. greatheadii* var. *davyana*, allowing unrestricted access by bees and other insects, but excluding all birds and small mammals; and iii) no visitors — exclusion of all potential visitors (i.e. birds, insects and mammals) using a fine gauze (<0.25 mm mesh) bag supported by a wire frame. All racemes were bagged and caged at the bud stage to avoid temporal bias and to exclude all visitors

Table 1
Floral characteristics of *A. greatheadii* var. *davyana* and *A. marlothii* complying with the bird pollination floral syndrome (Faegri and Van der Pijl, 1979; Thomson et al., 2000).

Ornithophilous syndrome	*A. greatheadii* var. *davyana*	*A. marlothii*
Vivid colours; bright reddish-orange flowers	Yes. Salmon pink to red flowers.	Yes. Bright orange to red flowers.
Long floral tube	Yes. Flower length=27.5±0.9 mm; stamen filaments loose in floral tube.	Yes. Flower length=32.7±0.4 mm; floral tube filled by stamens.
Exserted anthers and stigma	Yes. Anthers exserted before stigma, maximum nectar standing crop during male phase.	Yes. Anthers exserted before stigma, maximum nectar standing crop during male phase.
Absence of odour and nectar guides	Yes. No landing platform.	Yes. No landing platform, inner tepals tipped deep purple to black.
Abundant nectar	Yes. 33.1±0.6 μl.	Yes. 248.0±10.5 μl.
Low concentration of nectar	Yes. 21.1±0.3%.	Yes. 12.1±0.4%.

Characteristic details from Human and Nicolson (2008) and Symes and Nicolson (2008). See also Fig. 1. Values given as mean±SE.
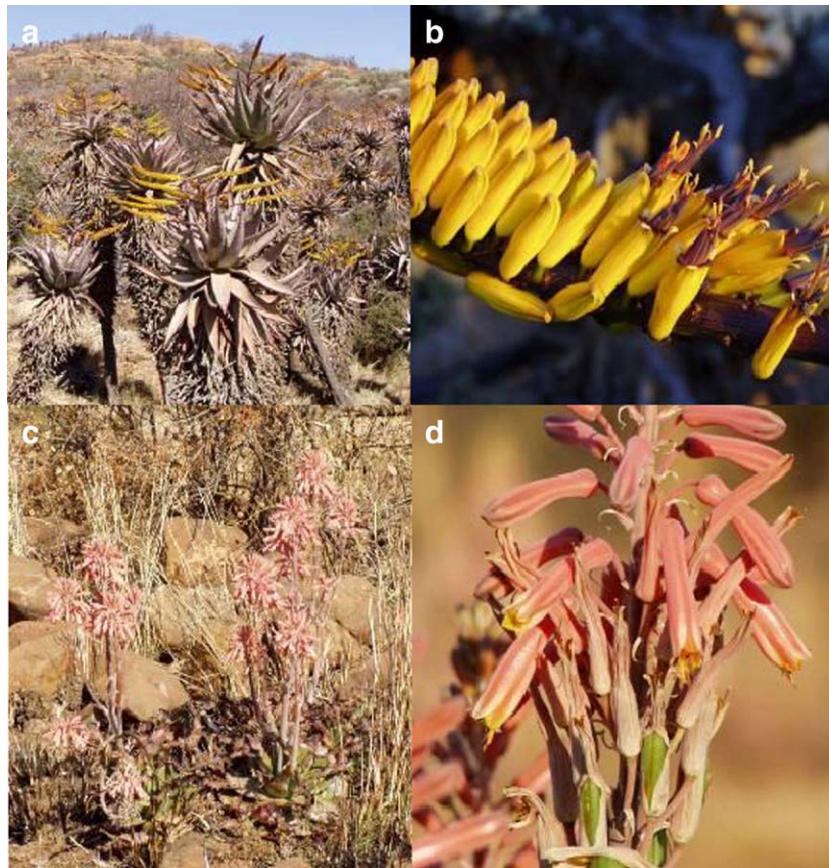
Fig. 1. *Aloe marlothii* plants (a) and flowers on raceme (b); *Aloe greatheadii* var. *davyana* plants (c) and raceme (d). Not adjusted to scale. See Table 1 for flower sizes. Photos: Craig Symes.

prior to flower opening. Racemes at different positions on a single inflorescence were selected for the three treatments. At the end of flowering, fruit set was calculated as the proportion of flowers on each raceme that developed into fruit. To determine seed production the number of seeds in five randomly selected fruits from each experimental raceme was counted.

Self-compatibility was assessed in five racemes of *A. marlothii* that were removed from separate plants and placed in water in the laboratory, and five racemes on separate *A. greatheadii* var. *davyana* plants in the field. In *A. marlothii*, where flowers on each raceme are densely packed, this isolation controlled for effects of other pollination events (e.g. wind). In *A. greatheadii* var. *davyana* racemes were covered with gauze bags (2 mm mesh size) to exclude pollinators in the field. Eight flowers on each raceme were tagged before opening; four flowers were then pollinated with pollen from another plant and four with pollen from the same plant. Pollen (from multiple donors) was dusted from an anther of a separate flower onto the stigma at least once during the female receptive phase (Symes and Nicolson, 2008; Human and Nicolson, 2008). Fruit development was then recorded for each tagged flower. Although the presence of seeds in each fruit was not confirmed, the size of fruit, in relation to fruit that contained seeds in the pollinator exclusion experiment, suggested that they would contain seeds.

2.3. Floral visitors

Avian visitors to aloe flowers were identified by observation. Feeding birds, or birds with pollen-dusted faces observed away from aloe plants, were recognised as potential pollinators. Pollen swabs were taken from the facial area of birds captured in mist nets, to identify nectar-feeding species that were not observed feeding on nectar or that did not have visible pollen on the head (Symes et al., 2008). Pollen was identified later under a microscope. Although the pollen grains of *A. marlothii* and *A. greatheadii* var. *davyana* may be indistinguishable, at the time of sampling these species were the only aloes flowering at the respective sites. Bill length of nectar-feeding birds and flower length (outside length from base of flower to tip of longest petal) of mature flowers was measured using Vernier calipers (0.1 mm).

2.4. Statistical analysis

Due to severe frost at Suikerbosrand in 2006, the majority of *A. marlothii* racemes did not set seed. Our data for fruit set and seed production were not normally distributed even after various transformations. Therefore, in order to assess the effect of different variables (species, year and treatment), the data were subjected to multivariate analyses that maximize the

variation *between* groups while minimizing variation *within* groups. General Discriminative Analysis was followed by non-parametric multiple comparisons of mean ranks (for all groups) in order to test for statistically significant differences within the groups. For comparisons of bill length and flower length we conducted *t*-tests. All statistical analyses were conducted using Statistica 6.0 (1984−2004). Data are expressed as means±SE.

3. Results

3.1. Fruit set and seed production

The effects of year (Wilks-λ=0.63; F=1.93; p<0.001), treatment (Wilks-λ=0.19; F=4.24, p<0.001), and species (Wilks-λ=0.41; F=4.68; p<0.001) were significant factors influencing fruit set in both *A. marlothii* and *A. greatheadii* var. *davyana*. The combined effect of the three variables (treatment, species and year) on fruit set of the two *Aloe* species was highly significant (Wilks-λ=0.43; F=1.68; p<0.001). Treatment and species as well as species and year combined had a significant effect on fruit set (Wilks-λ=0.33; F=2.41; p<0.001 and Wilks-λ=0.51; F=3.18; p<0.001) but not treatment and year (Wilks-λ=0.52; F=1.26; p=0.06).

There were significant differences between the percentage fruit set of the three different treatments for both *A. marlothii* and *A. greatheadii* var. *davyana* ($H_{5, 120}$=59.23, p<0.001) (Fig. 2). The year of treatment did not have a significant effect on fruit set in *A. greatheadii* var. *davyana* ($H_{1, 120}$=1.95, p=0.16) but did have a significant effect for *A. marlothii* ($H_{1, 120}$=12.03, p<0.001). Significant differences between treatments for each species are indicated in Fig. 2.

Seed production was significantly affected by year (Wilks-λ=0.83; F=2.07; p<0.001), treatment (Wilks-λ=0.43; F=5.18, p<0.001), and species (Wilks-λ=0.41; F=14.14; p<0.001). Not only did all three variables combined have a significant effect on seed production (Wilks-λ=0.79; F=1.27; p<0.001) but also all paired combined variables: treatment and species (Wilks-λ=0.59; F=2.98; p<0.001); species and year (Wilks-λ=0.78; F=2.83; p<0.001) and treatment and year (Wilks-λ=0.76; F=1.44; p<0.001).

In both *Aloe* species there were significant differences between seed production in the various treatments ($H_{5, 120}$=483.12, p<0.001). Significant differences were observed in seed production between years for *A. marlothii* and *A. greatheadii* var. *davyana* ($H_{5, 60}$=222.78, p<0.001). Significant differences between treatments for each species are indicated in Fig. 3.

In *A. marlothii* and *A. greatheadii* var. *davyana* fruit set in 20 cross-pollinated plants (25% and 33% respectively) was greater than in 20 self-pollinated plants (5% for both species) indicating both to be self-incompatible.

3.2. Floral visitors

At Suikerbosrand, where more comprehensive surveys were conducted, 39 bird species (including two sunbird species) were recorded feeding on *A. marlothii* (see Symes et al., 2008 for sampling techniques and procedures). Some birds such as red-
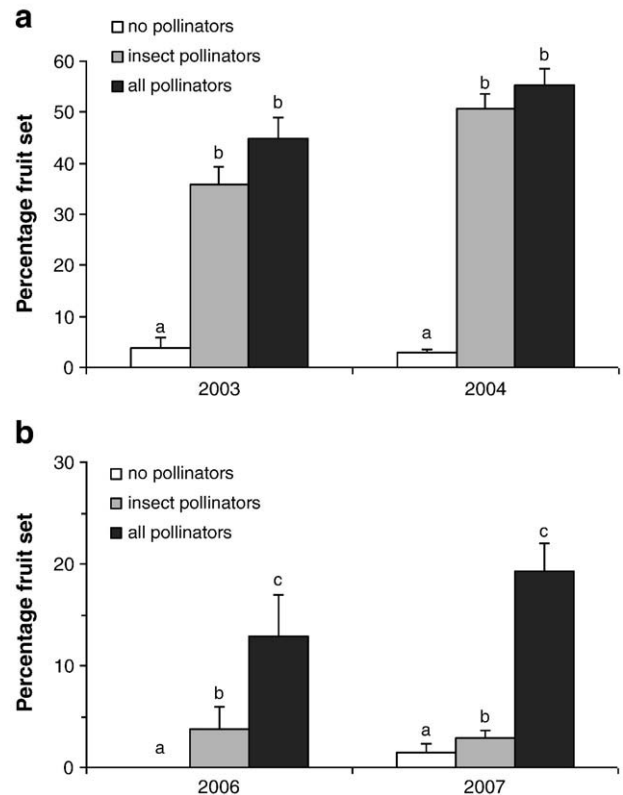

Fig. 2. Percentage fruit set (mean±SE) for different classes of pollinators in (a) *Aloe greatheadii* var. *davyana* and (b) *Aloe marlothii*, calculated from the number of flowers on each raceme that set fruit for different classes of pollinators (n=20 for each plant, each year). Letters indicate treatment comparisons for each species, with years considered separately (multiple comparisons, 2-tailed, p value significant at 0.05). Note different axis scales.

faced mousebird *Urocolius indicus* and streaky-headed seedeater *Serinus gularis* fed on flower parts. Birds climbed over the secund flowers to access nectar, which caused pollen to be deposited on the feet and belly as well as the facial area when probing; this was often visible as a bright orange wash on the plumage. Pollen was not observed on the facial area of malachite sunbirds, but only on the bill tip, suggesting a reduced role in pollination.

At Roodeplaat 11 bird species (including two sunbird species) were recorded feeding on nectar of *A. greatheadii* var. *davyana*. Observations of avian visitors at this site were less intensive and the number of species feeding on *A. greatheadii* var. *davyana* nectar is likely to be higher, but probably less than that of *A. marlothii*. When feeding on *A. greatheadii* var. *davyana* nectar, birds usually perched on the raceme beneath flowers in order to probe mature flowers that hang downwards. Birds either probed flowers for nectar or removed flower parts (e.g. speckled mousebird *Colius striatus* and southern masked-weaver *Ploceus velatus*) to feed on them or to reach the less accessible nectar. In doing so some birds may have damaged reproductive parts.

The bill lengths of birds observed feeding on *A. greatheadii* var. *davyana* nectar were significantly shorter than flower length (*t*-test, p<0.05). For birds that fed on *A. marlothii*, all captured species except two (malachite sunbird and common scimitarbill *Rhinopomastus cyanomelas*) had bills shorter than
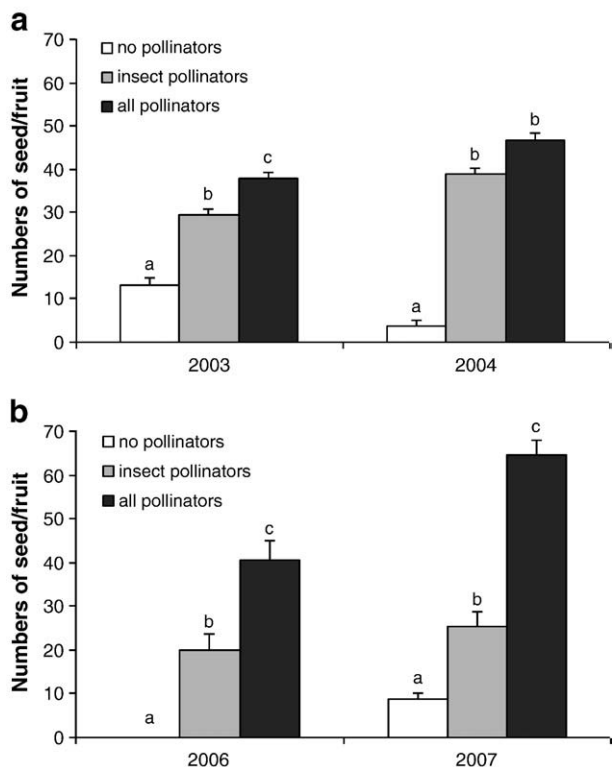
Fig. 3. Seed production per fruit (mean±SE) for different classes of pollinators in, (a) *Aloe greatheadii* var. *davyana* and, (b) *Aloe marlothii*. Letters indicate treatment comparisons for each species, with years considered separately (multiple comparisons, 2-tailed, *p* value significant at 0.05).

aloe flowers (*t*-test, $p < 0.05$). Of these species, the malachite sunbird ($n = 1$), like those that visit *Kniphofia caulescens* (Brown et al., 2009-this issue), did not have pollen visible on the facial area, whilst common scimitarbill ($n = 2$) did. Bills ranged in length from 8.7 mm in the black-throated canary *Serinus atrogularis* to 43.4 mm in the common scimitarbill, and included a wide variety of different bill shapes.

Bird visitations to *A. marlothii* are summarized in Symes et al. (2008). Insects were seldom, if ever, seen feeding on *A. marlothii* nectar. For *A. greatheadii* var. *davyana* we have no quantitative data for flower visitations by birds but did observe passerine birds being the early visitors while sunbirds and honeybees visited throughout the day.

4. Discussion

The flowers of *A. greatheadii* var. *davyana* and *A. marlothii* conform well to a bird pollination syndrome. Although exclusion experiments did not enable direct measurement of the contribution of birds to pollination in these species, fruit set in *A. greatheadii* var. *davyana* was similar for insects and for insects and birds combined, suggesting a negligible contribution by birds. In *A. marlothii*, fruit set due to insects only was similar to the no-pollinator treatment, and significantly less than the control (all-pollinator) treatment, suggesting that the role of birds was most important for this species. In *A. greatheadii* var. *davyana* the insect contribution to pollination is assumed to be

mostly due to honeybees, whilst in *A. marlothii* pollination by birds is carried out by a host of at least 83 species of generalist avian nectarivores (Oatley, 1964; Oatley and Skead, 1972; Symes, 2008; Symes et al., 2008).

A number of studies have tested whether ornithophilous pollination syndromes correctly predict the floral visitors and primary pollinators of plant species. In Tasmania, pollination syndromes are generally unreliable predictors of visitors (Hingston and McQuillan, 2000) and in two New Zealand mistletoes (*Peraxilla colensoi* and *P. tetrapetala*), which display a classic ornithophilous syndrome, both bees and birds were found to be pollinators (Robertson et al., 2005). Hargreaves et al. (2004) showed that birds were mainly responsible for the pollination of *P. roupelliae* and that insects play only a minor role. Therefore, although pollination syndromes are valuable for the development of testable hypotheses about pollination systems they should not be accepted as evidence establishing the primary pollinators of a plant (Hargreaves et al., 2004).

Little is known of the pollinators of the at least 450 *Aloe* species in the Afrotropical region (Reynolds, 1969; Glen and Hardy, 2000; Reynolds, 2004; Van Wyk and Smith, 2005). An assessment of 125 *Aloe* species by Botes (2007), based on floral characteristics, showed that those flowering predominantly during summer months are putatively insect-pollinated, whilst those flowering during winter are likely pollinated by occasional nectarivores and those flowering throughout the year by true nectarivores (sunbirds). However, for most of these species the pollinator types have not been critically investigated and it is not unreasonable to assume that exceptions exist. For example, *A. ferox*, which occupies a similar ecological niche to *A. marlothii* in the south-east of South Africa, produces similar nectar (180 μl; 12.5% w/w), and Hoffman (1988) showed that its flowers were visited by both specialist (sunbirds) and generalist avian visitors as well as honeybees (overall fruit set = 27%), although pollinator exclusion experiments were not conducted to determine the role of each of these guilds. Experiments have been conducted on *A. candelabrum* (synonymous with *A. ferox*); here both generalist and specialist birds were identified as the most important pollinators, with the role of insects being insignificant (Stokes and Yeaton, 1995). In five arborescent *Aloe* species with ornithophilous flowers honeybees were frequent visitors but ineffective pollinators (Botes et al., 2009). Two smaller island endemic species (*A. divaricata*, 15% fruit set; *A. mayottensis*, 30% fruit set), similar in size to *A. greatheadii* var. *davyana*, are each pollinated by a sunbird species, with a minor pollination role attributed to bees and other insects (Ratsirarson, 1995; Pailler et al., 2002).

Aloe maculata has flowers suggestive of a bird pollination syndrome, yet is pollinated by birds and bees (S.D. Johnson, pers. comm.). In *A. inconspicua*, small white flowers produce minute amounts of nectar (0.1 μl), and the main pollinator is a bee, *Amegilla fallax* (Hargreaves et al., 2008); however, these flowers do not suggest a bird pollination syndrome. *Aloe pruinosa*, a summer flowering aloe with typical bird pollination floral traits, produces nectar (mean concentration 19.7% and volume 15 μl) similar to that of *A. greatheadii* var. *davyana*,

and is visited by both birds and bees; insects also contribute to its pollination (Wilson et al., 2009). These results, as well as our data for *A. greatheadii* var. *davyana*, contradict the bird pollination syndrome suggested by floral traits and indicate that honeybees can play an important role in pollination of some aloes.

Although nectar volume and concentration may be broadly associated with certain classes of visitors, other factors serve to filter flower visitors. Nectar of *A. marlothii* is relatively dilute, so may be unattractive to specialist avian nectarivores that are less efficient pollinators (Johnson and Nicolson, 2008). *Aloe vryheidensis*, a winter-flowering aloe with conspicuous inflorescences, produces dilute nectar (6–17%) that attracts generalist birds; in this case specialist sunbirds are inefficient pollinators because of their long bills, and honeybees are deterred by the bitter taste of the dark nectar (Johnson et al., 2006).

In five sympatric winter-flowering *Aloe* species in the Eastern Cape, South Africa, the specialist–generalist bird pollination community is structured according to nectar properties, floral architecture and pollen deposition sites (Botes et al., 2008). These aloes, like *A. marlothii* and *A. greatheadii* var. *davyana*, are self-incompatible, and effective cross pollination is required for successful seed set (Brandham, 1969; Riley and Mujamdar, 1979; Botes et al., 2009). Two of them (*speciosa* and *ferox*) have short densely packed flowers (as in *A. marlothii*) attracting generalist birds, while another two (*pluridens* and *lineata* var. *muirii*) have longer, loosely pendant flowers attracting sunbirds (Botes et al., 2009). This dichotomy is mirrored in the differences between our two study species. However, although specialist avian pollinators (sunbirds) were observed at the Roodeplaat study site, their contribution to pollination of *A. greatheadii* var. *davyana* may be outweighed by that of abundant honeybees. When collecting nectar, honeybees are able to crawl into the floral tubes of *A. greatheadii* var. *davyana* flowers, like those of *A. pluridens* (Botes et al., 2009), but not into *A. marlothii* flowers where the anther filaments limit access. Floral features and bee behaviour determine whether or not bees are effective pollinators, and exclusion of birds from inflorescences of *A. greatheadii* var. *davyana* clearly demonstrates the importance of honeybees for pollination of this species.

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