

Good times, bad times: inter-annual reproductive output in a montane endemic succulent (*Aloe peglerae*; Asphodelaceae) driven by contrasting visitor responses of small mammals and birds

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Abstract. The movements of birds and small mammals may be affected by spatial and temporal variation in resource availability. For the genus *Aloe*, bird abundance and diversity increase in response to increases in nectar availability during flowering. *Aloe peglerae* Schönland, endemic to the Magaliesberg Mountain Range, South Africa, is primarily pollinated by the Cape rock-thrush (*Monticola rupestris*), but the nocturnal Namaqua rock mouse (*Micaelamys namaquensis*) contributes to pollination. To test the independent contributions of different pollinator guilds, i.e. birds and small mammals, we conducted selective pollinator exclusion experiments during two consecutive flowering seasons – one ‘good’ year and one ‘poor’ year (14 and 7% of plants flowering respectively). Reproductive output for both years was measured for *A. peglerae* plants assigned to selective exclusion treatments: (i) no visitors; (ii) nocturnal visitors; (iii) diurnal visitors; and (iv) all visitors, with camera traps recording visitors to each treatment. Bird visitation rates to the ‘diurnal visitors’ treatment were higher during the good year; subsequently, reproductive output in the poor year was lower, with plants in this treatment producing no fruit in the poor flowering year. In the ‘nocturnal visitors’ treatment, nocturnal visitation rates were similar with no significant difference in reproductive output between years. Seed viability was maintained between years, although less seed was produced during the poor flowering season. Mobile birds are less abundant in the *A. peglerae* population during poor flowering years – years when nectar resources are less abundant than in good flowering years, resulting in reduced plant reproductive output. However, the presence of non-flying, small mammals that cannot relocate to better feeding grounds compensates for the absence of birds in poor flowering years. This aloe may be resilient against Allee effects in the absence of primary pollinators. Nonetheless, conservation of *A. peglerae* should still be prioritised since low flowering densities and ongoing anthropogenic disturbance could be detrimental to the species’ survival.

Additional keywords: Cape rock-thrush, inter-annual variation, Namaqua rock mouse, resource tracking.

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Introduction

Animals move across landscapes in search of suitable breeding areas, mates and food resources (Wilshurst *et al.* 1999; Carter 2004; Tellería and Pérez-Tris 2007; Dzerefos *et al.* 2015). The ability of birds to move effectively between patches in space and time has been well documented, and is facilitated by their ability to fly (e.g. Brown and Hopkins 1996; Franklin 1999; Malizia 2001; Cotton 2007; Symes *et al.* 2008; Las-Casas *et al.* 2012). This movement can occur at multiple spatial scales as defined by a species’ diet, e.g. frugivore, insectivore or nectarivore (Loiselle and Blake 1991; Craig and Hulley 1994; MacNally 1996; Johnson and Sherry 2001; García and Ortiz-Pulido 2004). Nectar is an important food source for birds during periods when other resources may become limited, and changes in the abundance of nectar feeders in response to fluctuations in nectar

availability have been recorded (e.g. Brown and Hopkins 1996; MacNally 1996; Symes *et al.* 2001, 2008; Cotton 2007; Forbes *et al.* 2009; Las-Casas *et al.* 2012; Kuiper *et al.* 2015). This is true of opportunistic and generalist nectarivores that make use of abundant nectar resources that specialists may be unable to completely exploit (Oatley and Skead 1972; Franklin and Noske 1999; Franklin 1999).

Small, non-flying mammals are less mobile and restricted to smaller home- and foraging ranges, compared with birds. Migrations over large distances in search of food are often energetically impractical and may also have increased predation risks (Schradin and Pillay 2006), which results in a higher dependence on resources in the immediate surroundings. This may also explain why some small flying mammals such as gliders and bats have evolved to include nectar as an important

part of their diet (e.g. Goldingay 1990). Recently, more studies have begun to highlight small mammal nectar feeding associations, and the contributions these non-flying species make towards plant pollination, despite their limited mobility (e.g. Fabaceae: Letten and Midgley 2009; Hyacinthaceae: Wester *et al.* 2009; Proteaceae: Johnson and Pauw 2014; Melidoniis and Peter 2015; Schmid *et al.* 2015; Steenhuisen *et al.* 2015; Zoeller *et al.* 2016).

The genus *Aloe* (Asphodelaceae) is widespread across subSaharan Africa, with the highest density and diversity found in southern Africa (Carter *et al.* 2011; Cousins and Witkowski 2012). Many aloes display a bird pollination syndrome, with tubular flowers, that range from yellow to red, and no discernible scent (Reynolds 1950; Van Wyk and Smith 2014). Numerous studies have highlighted the importance of birds as pollinators of aloes (e.g. Hoffman 1988; Botes *et al.* 2008; Botes *et al.* 2009b; Symes *et al.* 2009; Hargreaves *et al.* 2012) with a few species pollinated by insects (e.g. Hargreaves *et al.* 2008; Botes *et al.* 2009a; Symes *et al.* 2009; Hargreaves *et al.* 2012; Duffy *et al.* 2014). Aloe nectar is an important food resource for birds, especially for generalist (opportunistic) species in dry, resource limited winters (Symes *et al.* 2008, 2011; Kuiper *et al.* 2015), with different pollinators showing preferences for nectar with different properties (Johnson *et al.* 2006; Johnson and Nicolson 2008). Specialist (true) nectarivores (e.g. sunbirds with long, narrow bills) are attracted to low volumes of concentrated nectar (10–30 μL , 15–25% w/w), whereas generalist or opportunistic nectarivores (e.g. short-billed birds) are attracted to dilute nectar which is produced in large volumes (40–100 μL , 8–12%; Johnson and Nicolson 2008).

Consequently, birds track the flowering periods of aloes, when nectar is most abundant (Symes *et al.* 2008; Forbes *et al.* 2009; Kuiper *et al.* 2015). Oatley (1964) noted that the number of bird species present and feeding in a stand of flowering *Aloe marlothii* plants increased in a year where the plants flowered well, as opposed to the previous year of lower flowering density. Symes *et al.* (2008) found that there was an increase in the abundance and diversity of nectar feeding bird species during the flowering season of *A. marlothii*, with some nectar feeding species only present during the flowering season. Most bird species that arrived during peak flowering were generalist nectarivores, whereas specialist nectarivores showed no significant change in abundance in response to changes in nectar availability (Symes *et al.* 2008). In contrast, Forbes *et al.* (2009) recorded an influx of both specialist and generalist nectar feeding birds at the onset of flowering in *Aloe ferox*. This influx was annual, consisting predominantly of Malachite Sunbirds (*Nectarinia famosa*) and *Ploceus* weaver species (Kuiper *et al.* 2015). During the peak flowering period, the number of birds increased between three and five times compared with the rest of the year (Kuiper *et al.* 2015). However, the peak flowering period of *A. ferox* did not influence the population and/or number of birds from other feeding guilds, i.e. frugivores and insectivores, suggesting that nectarivores are responding to the peak in nectar availability by tracking resources (Kuiper *et al.* 2015).

Aloe peglerae Schönland is a critically endangered stemless aloe, endemic to the Magaliesberg Mountain Range, South Africa (Reynolds 1950; Van Wyk and Smith 2014; Pfab *et al.* 2016). The aloe produces a single raceme with red tubular

flowers producing copious amounts ($47 \pm 7 \mu\text{L}$; mean \pm s.e.) of dilute ($10.2 \pm 0.5\%$ w/w; mean \pm s.e.) nectar (Payne *et al.* 2016). Although not explicitly tested, exclusion of all biotic visitors suggests that *A. peglerae* is self-incompatible (Arena *et al.* 2013; Payne *et al.* 2016), and like many *Aloe* species (e.g. Hoffman 1988; Botes *et al.* 2009b; Symes *et al.* 2009; Wilson *et al.* 2009), is reliant on external pollen vectors. The flowers are typical of a bird pollination syndrome (Faegri and van der Pijl 1979), and exclusion experiments, with low seed set in bird exclusions, have shown birds to be the primary pollinators (Arena *et al.* 2013; Payne *et al.* 2016). The Cape rock-thrush (*Monticola rupestris*) accounts for ~68% of visits (Payne *et al.* 2016) and up to 60% of probing visits (Arena *et al.* 2013). Recently, small mammals, although less effective than avian pollinators, have been shown to successfully pollinate *A. peglerae* at night, with the Namaqua rock mouse (*Micaelamys namaquensis*) an important nocturnal visitor (9.6% of visits; Payne *et al.* 2016).

Aloe peglerae flowering is annual at a population level, but variable at an individual level, with fruit and seed production more irregular than flowering (Scholes 1988; Arena *et al.* 2013). It is unknown to what extent the variability of flowering frequency affects pollinator abundance, and what subsequent effect this may have on visitation by these two different pollinator guilds, i.e. diurnal birds and nocturnal small mammals, and on aloe reproductive output. Thus, the aim of this study was to investigate the effect of annual variation in the proportion of flowering *A. peglerae* plants on reproductive output (fruit set, seed set, total seed production, and seed viability) by birds and small mammals, as determined from selective pollinator exclusion experiments. Since birds are known to track resources and aggregate in areas with increased nectar availability, it was predicted that fewer birds would be present in poor flowering years when nectar rewards are low. It was expected that this would consequently result in decreased reproductive output of exclusively bird-pollinated plants. In contrast, small mammals that are less mobile, would be expected to remain restricted to their home ranges (e.g. Ribble and Perrin 2005), and reliant on resources in their immediate environments. We expected this to result in an increase in overall visitation rates by small mammals in poor flowering years, since fewer plants were flowering and more small mammals may be visiting (more frequently) at the same plants. A consequent increase in reproductive output for plants visited exclusively by small mammals in poor flowering years was expected. Although interactive effects of diurnal birds and nocturnal small mammals were more difficult to predict, our experimental design addressed this.

Materials and methods

Study site and species

This study was conducted in the Peglerae Conservancy (1650 m above sea level), in the Magaliesberg Mountain Range, ~25 km west of Pretoria, South Africa. The Conservancy was established to protect *Aloe peglerae* Schönland from anthropogenic disturbances, such as habitat transformation and the unregulated and illegal harvesting of seed and whole plants, as well as to facilitate monitoring for conservation (Pfab and

Scholes 2004; Wesson 2007). The site occurs in Gold Reef Mountain Bushveld (Mucina and Rutherford 2006), with shallow soils dominated by grasses, shrubs and scattered trees (Mucina and Rutherford 2006; Arena *et al.* 2013, 2015). Rainfall is seasonal, falling mostly in summer, but can vary significantly between years (530 mm in 2013, and 289 mm in 2014; South African Weather Service 2016). The Conservancy (~56 ha) has a mean density of 142 *A. peglerae* plants ha⁻¹ in the areas where *A. peglerae* is found (~5 ha; Arena *et al.* 2015).

Adult *A. peglerae* plants (>20 cm in diameter) produce a single raceme of densely packed, tubular flowers during winter (June–July; Scholes 1988; Fig. 1a). Flowers (~30 mm in length) are dull red in bud, and become a yellowish-green with deep purple stamens and exerted anthers (~25 mm past the mouth) when mature (Scholes 1988; Van Wyk and Smith 2014; Fig. 1a). These exerted anthers, along with the long, tubular corollas of the flowers suggest bird pollination, as was confirmed by exclusion experiments (Botes *et al.* 2009b; Hargreaves *et al.* 2012; Arena *et al.* 2013). Flowers open sequentially from the base of the raceme, over ~15 days (Payne *et al.* 2016).

Visitation rates

Vertebrate visitation rates were measured through selective exclusion experiments conducted during the flowering seasons of 2013 (14% of *A. peglerae* plants flowering, representing a ‘good’ flowering year) and 2014 (7% flowering, representing a ‘poor’ flowering year). These flowering proportions in the population compare to the average of 29% of plants that have flowered per year over five flowering seasons, with the proportion of flowering plants declining in each year (C. T. Symes, unpubl. data; Arena 2013). In previous studies of the same population, individual plants were labelled with an engraved metal identification tag and their locations recorded with a handheld GPS (Garmin, GPSMAP 60Cx. USA; Arena *et al.* 2013; Payne *et al.* 2016), resulting in a total of 609 plants. Before flower opening, 14 and seven *A. peglerae* plants in 2013 and 2014, respectively, were assigned to each of the following selective exclusions:

- (i) no visitors treatment (NOVIS_{TRT}) – plants covered with mesh cages (that exclude visitors of all types, including insects) for the entire duration of the flowering season, excluding all visitors (diurnal and/or nocturnal) from visiting flowers;
- (ii) nocturnal visitors treatment (NOCT_{TRT}) – plants covered with mesh cages during the day and uncovered at night to allow visitation by nocturnal visitors;
- (iii) diurnal visitors treatment (DIUR_{TRT}) – plants covered with mesh cages at night, and uncovered during the day to allow for visitation by diurnal visitors; and
- (iv) all visitors (control) treatment (ALL_{TRT}) – plants uncovered for the entire flowering season, allowing diurnal and nocturnal visitor access to flowers.

Exclusion cages, large enough to not touch the flowers, were constructed from a bamboo tripod frame (height = ~0.9 m, basal area = ~0.3 m², fig. 1b in Payne *et al.* 2016), and covered with a pale brown, fine nylon mesh (1 mm² pores), which excludes all visitor types, including insects. Cages were secured along all

edges with large rocks, to prevent visitors accessing the plants. Effectiveness of cages was tested with camera traps focusing on NOVIS_{TRT} aloes, and a mouse was identified trying to access the plant but could not get through the cage. In 2013, aloes in close proximity shared cages, i.e. a NOCT_{TRT} and a DIUR_{TRT} aloe shared a cage, since treatments required cages at different times, facilitating the efficient moving of cages at dusk and dawn. In 2014, lower numbers of flowering aloes allowed for a cage to be assigned to each plant. Care was taken when placing or removing cages, to avoid pollen transfer between aloes via the mesh. Cages do not significantly alter microhabitat temperature within the cage (Payne *et al.* 2016).

Sampling lasted for four-five weeks in both seasons (25 June–27 July 2013; 02 July–30 July 2014). The same plants could not be sampled in both years due to the annual flowering variability. Although 42 plants were recorded as flowering in 2014, only seven plants were sampled per treatment, due to the unsuitability of some individuals for the experiment (e.g. damaged inflorescences).

An animal was considered a visitor if it touched the aloe in any way (the inflorescence and/or the leaves), since it had the potential to transfer pollen, due to the close proximity of the raceme and flowers to the leaves. The date and time of each visit was recorded, and each individual was identified to species, where possible. An individual was recorded as a ‘new visitor’ if the period between photographs was >30 s, or if the visitor was identified as a different individual (e.g. aberrant feather positioning or unique feather markings on birds). Often a visitor was acknowledged as the same individual when it remained in the same position in successive (3 s intervals) photographs. Mean visitation rates were calculated as the number of visitors per 1000 plants h⁻¹ (Payne *et al.* 2016).

Camera traps and exclusion cages were changed daily within an hour at dawn (06:45–07:45 hours) and within an hour at dusk (16:30–17:30 hours). These timings were chosen to select for the visitors relevant to each treatment, but in the transition from day to night and night to day, some visitors (e.g. birds feeding on NOCT_{TRT} aloes during the early morning or late evening) could not be controlled for (see later; Payne *et al.* 2016). The diurnal period was defined as 07:00–17:59 hours, and the nocturnal period as 18:00–06:59 hours; small mammals and birds visiting during each of these periods respectively were defined as ‘inappropriate’ visitors. Cages that were destroyed by baboons and/or strong wind ($n = 3$), or by fire (21 July 2014) were replaced with new, undamaged cages in the next changeover period, i.e. within 12 h. During fires before flowering in June 2013 (J. Wesson, pers. comm.) and on 21 July 2014, plants suffered little damage, apart from slight burning of some outer leaves (S. L. Payne, pers. obs.; Arena *et al.* 2015).

Reproductive success

Pollinator contributions were defined using measures of reproductive success, i.e. fruit set, seed set (average seed fruit⁻¹), total seed production plant⁻¹ and seed flower⁻¹. In 2013, reproductive success was measured for only 12 of the plants per treatment, as two racemes went missing in each treatment (possibly destroyed by baboons, S. L. Payne, pers. obs.). In 2014, reproductive success was measured for seven



Fig. 1. (a) A flowering *Aloe peglerae* plant, with red buds and greenish-yellow mature flowers, and exerted anthers and stamens; (b) a male Cape rock-thrush (*Monticola rupestris*) feeding on *A. peglerae* nectar and likely pollinating the flowers; (c) a sengi (*Elephantulus* sp.) standing on an *A. peglerae* plant at night; (d) an *A. peglerae* plant that produced fruit, densely packed on the raceme. Photographs: (a, d:) S. L. Payne photographs; (b, c) camera trap photographs. All scale bars = 10 cm.

plants in the ALL_{TRT}, five in the DIUR_{TRT} (two racemes missing), six in the NOCT_{TRT} (one raceme missing) and seven in the NOVIS_{TRT}. Approximately five weeks after the end of the flowering season (9 September 2013; 5 September 2014), fruit were removed from each of the racemes and counted.

A maximum of five whole fruit were randomly selected from each plant, and the remaining fruit were scattered around the site (Arena *et al.* 2013; Payne *et al.* 2016). The number of flowers on each raceme, represented by the number of peduncles (Symes *et al.* 2009; Arena *et al.* 2013; Payne *et al.* 2016) was counted, and

the fruit set of each aloe was calculated by dividing the number of fruit produced by the number of flowers. The mean number of flowers per plant for each treatment was also calculated and compared between treatments and years.

Harvested fruit were returned to a laboratory at the University of the Witwatersrand, and allowed to dehisce for ~5 weeks in separate, open brown paper bags (57 × 85 × 170 mm) at ambient temperature. The number of seeds in each dehiscent fruit was then counted and the mean number of seed fruit⁻¹ (seed set) determined for each plant. The estimated total seed production plant⁻¹ was calculated by multiplying the mean seed set for each plant by the number of fruit produced by that plant. Seeds flower⁻¹ was calculated by dividing total seed production by the number of flowers produced per plant.

Germination trials and seed viability

A maximum of 10 seeds from each fruit were randomly selected and pooled for each plant. Seeds were placed in labelled, sterilised Petri dishes on top of two sheets of filter paper and covered with one sheet of filter paper (Boeco Germany, Grade 3 hw, 65 g m⁻², 90 mm diameter). Petri dishes were kept saturated with distilled water in an environmental control chamber with a 12-h day-night cycle, with daytime temperatures of 25°C and night-time temperatures of 15°C and RH of 50% (Arena *et al.* 2013). Germinating seeds, identified by a radicle protruding by ≥2 mm (ISTA 2003), were counted every day for 3 weeks, and then three times a week for a further 3 weeks thereafter (Arena *et al.* 2013). Germinated seeds were removed, placed in separate Petri dishes and allowed to grow, with the intention of planting the seedlings back in The Peglerae Conservancy. Cumulative percentage germination was calculated as the percentage of seeds within each treatment that had germinated over the entire 6-week period.

After 6 weeks, seeds that had not germinated were removed from the control chamber. Empty seed coats were removed and these seeds recorded as 'dead', whereas remaining seeds were sliced in half to expose the embryo and immersed in a 1.0% 2,3,5-triphenyltetrazolium chloride (tetrazolium) solution overnight. The following day, seeds with pale pink embryos were recorded as 'viable', and seeds with embryos that remained white were considered 'dead' (ISTA 2003). Total seed viability per plant (%) was calculated as the sum of all germinated seeds and viable seeds after tetrazolium testing, divided by the number of seeds tested per plant for each treatment.

Mean germination time (MGT) was calculated using the following equation:

$$\text{MGT} = \frac{\sum Dn}{\sum n} \quad (1)$$

where D is the number of days since the beginning of germination, and n is the number of seeds germinated on day D (Zanjan and Asli 2012).

Data analysis

All data were tested for normality using Shapiro-Wilk normality test. The effect of treatment and year on overall treatment visitation rates and vertebrate guild visitation rates (birds vs small mammals in the NOCT_{TRT} and ALL_{TRT} only; visits 1000 plants⁻¹ h⁻¹) were separately modelled with generalised linear

models (GLM), with visits modelled as count data, with an offset for hours of sampling effort. Treatment or guild, and year were predictor variables, and a Poisson or Quasi-Poisson distribution (to account for over-dispersion), and a log-link function were specified. Although models did not fit data properly due to high variation within each treatment and small samples sizes (particularly in 2014), residuals were random and so GLM analyses were retained. A non-parametric Mann–Whitney U-test was used to test for significant differences between years in visitation rates of the most common diurnal and nocturnal visiting vertebrate species in each treatment.

Average number of flowers plant⁻¹ was compared between treatments in each year with a non-parametric Kruskal–Wallis rank sum test, and between years for each treatment with a parametric Student's t -test. Fruit set, average seed fruit⁻¹ (seed set), total seed production and seed flower⁻¹ were compared between treatments in each year using a non-parametric Kruskal–Wallis rank sum test, and between years for each treatment using a non-parametric Mann–Whitney U-test. Kruskal–Wallis multiple comparison *post-hoc* tests in the package 'pgirmess' were performed on datasets with significant differences ($P < 0.05$; Giradoux 2018). GLMs were not used to test for differences in reproductive success between treatments and years, due to the large number of zeros in each treatment (plants that produced no fruit, and therefore no seed), particularly in the poor flowering year, which meant that the models did not fit the data.

To compare cumulative percentage germination, MGT and total viability among treatments for 2013 and 2014, the results for both years were combined for each treatment, as a result of the small sample size for germination trials in 2014 ($n = 1$, $n = 0$ and $n = 2$ plants produced seed in the NOCT_{TRT}, DIUR_{TRT} and ALL_{TRT} respectively). Treatments were compared using a non-parametric Kruskal–Wallis rank sum test. Total viability of seeds produced by plants in each treatment was compared between years with a Chi-square test for Independence with Yates' continuity correction. *Post-hoc* tests, if necessary, were performed as above. All statistical analyses were performed in R (ver. 3.5.1; R Core Team 2018), with graphics created using the R package 'ggplot2' (Wickham 2016). Data are presented as mean ± s.e.

Results

Seasonal visitors and visitation rates

A total of 17 species (12 bird, four mammal and one reptile) visited *A. peglerae* plants across the four exclusion treatments in both years (see Supplementary Material table S1, available at the journal's website). Most ALL_{TRT} plants received both bird and small mammal visits in both years, with the exception of one plant in 2013 and one in 2014 receiving only bird visitors. All DIUR_{TRT} plants received only bird visitors in both 2013 and 2014, with one plant receiving no visitors in 2014. In 2013, nine of 11 NOCT_{TRT} plants received small mammal visits and at least one avian visit, and two plants received no visitors. In 2014, three NOCT_{TRT} plants received visits from both birds and small mammals, one plant received visits from small mammals only, three received only avian visits and one received no visits at all. Camera and exclusion cage changeover times did

Table 1. Visitation rates (visitors 1000 plants⁻¹ h⁻¹) for two different pollinator guilds (birds and small, non-flying mammals) for *Aloe peglerae* plants in selective exclusion treatments, in two successive flowering seasons with differing proportions of flowering plants

2013 represents a 'good' flowering year, and 2014 represents a 'poor' flowering year. Visitation rates were converted to visits 1000⁻¹ plants h⁻¹ to account for rates within the entire *A. peglerae* population. Abbreviations: NOCT_{TRT}, DIUR_{TRT}, and ALL_{TRT} = nocturnal, diurnal, and all visitors treatments respectively. Coefficients of variation (CVs) are presented, and emphasise the high variability within each treatment. Appropriate visitors, i.e. birds on DIUR_{TRT} plants, small mammals on NOCT_{TRT} plants, and both guilds on ALL_{TRT} plants, to each treatment are in bold text. Values are presented as means ± s.e.

	2013 (visits 1000 plants ⁻¹ h ⁻¹)	2014 (visits 1000 plants ⁻¹ h ⁻¹)
NOCT_{TRT}	59.17 ± 20.33	63.56 ± 21.11
Coefficient of variation	94.00%	113.90%
Birds	16.34 ± 3.54	37.64 ± 14.78
Small mammals	42.44 ± 24.86	24.86 ± 14.68
DIUR_{TRT}	167.18 ± 23.75	75.18 ± 19.19
Coefficient of variation	49.20%	67.50%
Birds	163.23 ± 23.78 ^A	75.18 ± 19.19
Small mammals	0	0
ALL_{TRT}	89.33 ± 13.27	131.58 ± 22.70
Coefficient of variation	44.60%	41.80%
Birds	80.33 ± 13.53	93.05 ± 19.78
Small mammals	7.83 ± 2.45	38.21 ± 10.99

^AThe total visitation rate of the DIUR_{TRT} in 2013 also includes visits from ground agama (*Agama aculeata*), resulting in the difference between the total visitation rate for the treatment and the visitation rate for the bird guild.

not differ significantly between years (Mann–Whitney U-test, NOCT_{TRT} start times: 2013: 16:45 hours, 2014: 16:58 hours; $U_{230} = 5876.0$, $P = 0.730$; NOCT_{TRT} end times: 2013: 07:47 hours, 2014: 07:46 hours; $U_{230} = 6071.5$, $P = 0.955$). In both years, 'inappropriate' avian visitors to the NOCT_{TRT} plants occurred either during sunrise just before the changeover period, or during the changeover period. To account for the effect birds may have had on NOCT_{TRT} aloe pollination, an 'inappropriate visitors correction' was applied to reproductive output data of plants in this treatment, where the proportion of visits by birds was subtracted from each measure of reproductive success (Payne *et al.* 2016). This did not make any significant difference to the statistical results so the original, uncorrected datasets were used. Cameras focussed on plants in the NOVIS_{TRT}, to confirm treatment (cage) effectiveness, did not record any visits to the plants in both 2013 and 2014, and therefore cages were deemed effective in fully excluding all potential pollinators.

Visitation rates were highly variable within each year, and this variability was maintained between years (Table 1). Visitation to the DIUR_{TRT} decreased significantly between years, whereas the other treatments remained unaffected by year (Table 2). A total of 98.1 and 100% of visits to the plants in the DIUR_{TRT} were made by birds, in 2013 ($n = 266$ visits) and 2014 ($n = 70$) respectively. A total of 70.2% of visits ($n = 131$) in 2013 and 33% of visits ($n = 75$) in 2014 to the NOCT_{TRT} were made by small mammals. Although visitation did not change significantly between years for either guild in the NOCT_{TRT}, small mammal visitation to the ALL_{TRT} increased between years (Tables 1 and 2).

Table 2. Results of general linear models (GLMs)

Parameter estimates (β), with standard errors (s.e.), and significance of each factor for overall treatment visitation rates, and guild visitation rates (birds vs small mammals) for the all visitors control treatment (ALL_{TRT}) and the nocturnal visitors treatments (NOCT_{TRT}) are presented. Visitation rates (the dependent variable) were modelled as count data, with an offset for hours of sampling effort, with Poisson or Quasi-Poisson distributions (to account for over-dispersion). In the overall treatment visitation rate model, the all visitors control treatment (Treatment (all visitors)) and 2013 (Year (2013)) are the reference categories for treatment and year factors respectively. In the guild visitation rate models, the bird guild (Guild (birds)) and 2013 (Year (2013)) are reference categories for the guild and year factors respectively. Significant differences are indicated: * $P < 0.05$. Large estimates and standard errors are due to high variation within treatments, and small sample sizes; however, residuals are random and therefore GLM analyses were retained

Predictors	Estimate (β) ± s.e.	P-value
<i>Treatment visitation rates</i>		
Intercept	-352.07 ± 506.86	0.49
Treatment (diurnal visitors)	1860.55 ± 887.87*	0.04*
Treatment (nocturnal visitors)	535.24 ± 935.38	0.57
Year (2014)	0.18 ± 0.25	0.49
Treatment (diurnal visitors): year	-0.92 ± 0.44*	0.04*
Treatment (nocturnal visitors): year	-0.27 ± 0.47	0.57
<i>Guild visitation rates</i>		
All visitors treatment (ALL _{TRT})		
Intercept	-2.55 ± 209.9	0.99
Guild (small mammals)	-1538 ± 503.2*	0.002*
Year (2014)	0.0017 ± 0.1	0.99
Guild (small mammals): year	0.76 ± 0.25*	0.002*
<i>Nocturnal visitors treatment (NOCT_{TRT})</i>		
Intercept	-1493.18 ± 1304.7	0.26
Guild (small mammals)	3258.26 ± 1905.88	0.1
Year (2014)	0.74 ± 0.65	0.26
Guild (small mammals): year	-1.62 ± 0.95	0.1

The Cape rock-thrush (Fig. 1b) was the most common diurnal visitor, accounting for ~80% of all visits in the DIUR_{TRT} (2013: $n = 214$ of 266 visits; 2014: $n = 56$ of 70 visits) in both years. Although the visitation rate of this species did not decrease significantly between years (ALL_{TRT}: $U_{14} = 20$, $P = 0.46$; DIUR_{TRT}: $U_{16} = 39$, $P = 0.38$), the overall percentage contribution to visitation in the ALL_{TRT} decreased from 68.2% ($n = 199$ of 292 visits) in 2013 to 52.4% ($n = 99$ of 189 visits) in 2014 (Supplementary material table S1). The Namaqua rock mouse was the most common nocturnal visitor, accounting for 66.4% in 2013 ($n = 87$ of 131 visits) and 26.7% in 2014 ($n = 20$ of 75 visits) of all visits in the NOCT_{TRT} (Supplementary material table S1). Percentage contribution to visitation by the Namaqua rock mouse in the ALL_{TRT} increased from 9.6% ($n = 28$ of 292 visits) in 2013 to 20.6% ($n = 39$ of 189 visits) in 2014. Although there was no significant change in Namaqua rock mouse visitation rates to the NOCT_{TRT} between the two seasons ($U_{14} = 58$, $P = 0.25$), the percentage contribution by this species to visitation decreased in the NOCT_{TRT}.

The visitation rates of the most abundant visitors per guild, i.e. three bird species (Cape rock-thrush, dark-capped bulbul (*Pycnonotus tricolor*), and streaky-headed seed-eater (*Crithagra gularis*)), and two small mammal species (Namaqua rock mouse and sengi (*Elephantulus* sp., likely *E. myurus* or *E. brachyrhynchus*; M. Perrin, H. Smit-Robinson, G. Rathbun,

pers. comm.; Fig. 1c) were compared within each treatment between 2013 and 2014. There were no significant changes in visitation rates of these species (Supplementary material table S2), with the exception of the streaky-headed seed-eater, which decreased, seeming to have disappeared altogether, in the DIUR_{TRT} in 2014, from 12.59 ± 2.95 to 0 visits $1000 \text{ plants}^{-1} \text{ h}^{-1}$ ($U_{17} = 73.5$, $P = 0.01$; Supplementary material table S2). Despite the presence of mountain wheatear (*Oenanthe monticola*) and mocking cliff-chat (*Thamnota cinnamomeiventris*), known to feed on *Aloe* nectar (Symes 2010), they were not recorded feeding on *A. peglerae* nectar in either flowering season.

Insects do not contribute significantly to the pollination of the aloe (Arena et al. 2013), and their activity and abundance (especially in the early morning) is low in winter (Symes et al. 2008). However, camera trap photographs recorded insects, presumably bees, around the flowers from 10:00 hours, with activity peaking at 12:00 hours and slowly declining from 15:00 hours (Arena et al. 2013). This contrasts with the peak visiting times of the Cape rock-thrush, an insectivore, where bird presence on the aloes increases between 07:00 and 08:00 hours, declined between 10:00 and 14:00 hours, and increased again at ~15:00 hours. This suggests that the birds (specifically the Cape rock-thrush) are feeding on nectar in the early morning and late afternoon to supplement their diet when insects, their primary food source, are inactive (Symes et al. 2008), switching to their optimal insect diet as it becomes available. However, no camera trap photographs recorded any birds noticeably or actively foraging for insects around the aloe, following the suggestion by Oatley (1964) that nectar is the primary attractant for birds, and the possibility of an insectivore finding prey at the aloe flowers is purely 'fortuitous'. This pattern in other bird species and feeding guilds, dependent on the primary diet of the particular species, requires further investigation.

Streaky-headed seed-eaters were recorded tearing perianths of flowers and consuming flowers (and possibly nectar) in 2013. The Namaqua rock mouse was destructive in both years, removing flowers at night. In the case of one NOCT_{TRT} aloe in 2013, mice removed several flowers each night, until the plant had no flowers left, and the aloe produced no fruit. In 2014, a NOCT_{TRT} aloe received no nocturnal visitors, until fire burnt the surrounding area. Thereafter, small mammals visited the plant and herbivory occurred, resulting in no fruit being produced. Baboons were recorded pulling on – but in these instances not damaging – inflorescences, twice in both years. Two DIUR_{TRT} aloes were visited by a ground agama (*Agama aculeata*) in 2013. The agama sat either on the flowers or leaves, and did not appear to feed on flowers or nectar. In 2014, one Smith's red rock rabbit (*Pronolagus rupestris*) was recorded once sniffing the inflorescence of a NOCT_{TRT} aloe, but no other contact with the aloes was recorded. Seven other mammal species were recorded by the camera traps in both years, but were not associating with the aloes and inflorescences in any way (Supplementary material table S3).

Reproductive success

Some inflorescences went missing or were destroyed in both years, while some aloes were exposed to a second fire during fruiting in 2014 (J. Wesson, pers. comm.) and no whole fruit was available for harvest (Table 3). Many aloes in 2014 showed evidence of fruit production, i.e. dry pieces of fruit capsule, or green peduncles or peduncle scars where fruit had been removed (Table 3). In these cases, fruit set could be calculated for these aloes, but seed set and total seed production could not.

The mean number of flowers plant^{-1} (2013: 241 ± 10 flowers plant^{-1} , $n = 48$ plants; 2014: 182 ± 11 flowers plant^{-1} , $n = 25$

Table 3. Reproductive success for *Aloe peglerae* plants in each selective exclusion treatment in two consecutive flowering seasons of differing flowering success, where 2013 represents a 'good' flowering year (14% of plant flowering), and 2014 represents a 'poor' flowering year (7% flowering)
Abbreviations: NOVIS_{TRT}, no visitors treatment; NOCT_{TRT}, nocturnal visitors treatment; DIUR_{TRT}, diurnal visitors treatment; ALL_{TRT}, all visitors treatment.
All values are presented as means \pm s.e.

	2013 NOVIS _{TRT}	2014 NOVIS _{TRT}	2013 NOCT _{TRT}	2014 NOCT _{TRT}	2013 DIUR _{TRT}	2014 DIUR _{TRT}	2013 ALL _{TRT}	2014 ALL _{TRT}
No. of plants in treatment	12	7	12	6 ^A	12	5 ^A	12	7
No. of missing/destroyed inflorescences	2	0	2	1	2	2	2	0
Average no. of flowers plant^{-1}	256 ± 26	183 ± 21	240 ± 15	157 ± 21	243 ± 16	167 ± 12	226 ± 20	214 ± 24
No. of plants with fruit burnt in fire	0	1	0	0	0	0	0	1
No. of plants with evidence of fruit ^B	0	0	0	1	0	0	0	3
No. of plants that produced harvestable fruit ^B	0	0	8	2	11	0	10	5
Average no. of fruit produced plant^{-1}	0	0	23 ± 7.7	9.5 ± 7.9	55 ± 11.1	0	41.5 ± 8.3	40.7 ± 22.2
Fruit set (%)	0	0	8.9 ± 2.7	4.9 ± 4.0	23.3 ± 4.9	0	19.9 ± 4.1	18.1 ± 9.6
Seed set (all flowering plants)	0	0	24.1 ± 5.5	5.0 ± 5.0	42.6 ± 4.3	0	43.4 ± 6.1	11.0 ± 7.2
Seed set (fruit producing plants only)	0	0	36.2 ± 3.2	14.7 ± 9.6	25.4 ± 4.8	0	52.0 ± 1.9	38.6 ± 5.8
Average seed production plant^{-1}	0	0	861 ± 321	242 ± 242	2433 ± 457	0	2129 ± 424	1270 ± 828
Average seed flower ⁻¹	0	0	10.4 ± 2.0	1.2 ± 1.2	3.3 ± 1.1	0	10.0 ± 2.0	6.1 ± 4.1

^ASeven plants were originally assigned to each treatment; however, from the end of field sampling, i.e. flowering period, to the fruit harvest, two racemes in the DIUR_{TRT} and one raceme in the NOCT_{TRT} went missing, presumably removed by baboons. Therefore, these plants could not be used for reproductive success calculations and were removed from the sample for these analyses.

^BThe number of plants with evidence of fruit were those which showed some indication of producing fruit, usually in the form of remaining pieces of fruit capsule on the raceme, or green peduncle scars where fruit had been recently removed. Fruit set, and consequently seed set, could not be calculated for these plants. The number of plants that produced harvestable fruit were those where fruit was still attached to the raceme at the time of harvest and fruit set could be calculated. Whole fruit could be harvested from these plants and seed set could be calculated as well.

plants) did not differ among treatments in each year (2013: $F_{3,44} = 0.37$, $P = 0.77$; 2014: $F_{3,21} = 1.38$, $P = 0.28$). However, inflorescences produced by plants in 2014 produced significantly fewer flowers than in 2013 for plants assigned to the DIUR_{TRT} ($t_{15} = 2.87$, $P = 0.01$) and the NOCT_{TRT} ($t_{16} = 3.25$, $P = 0.01$; Table 3).

In 2013, most plants in each treatment produced fruit (Fig. 1d), whereas in 2014 the majority of sampled plants produced no fruit, despite receiving visitors during flowering (Table 3). Plants in the NOVIS_{TRT} produced no fruit in either year and, therefore, no seed could be harvested. Fruit set differed significantly between the ALL_{TRT} (19.9%) and both the DIUR_{TRT} (23.3%) and the NOVIS_{TRT} (0.0%) in 2013 ($H_{3,44} = 23.31$, $P < 0.0001$), but not between the NOCT_{TRT} (9.0%) and the DIUR_{TRT} or the NOVIS_{TRT}, as indicated by *post-hoc* testing. Although there was an overall significant difference in mean fruit set among treatments in 2014 ($H_{3,24} = 10.48$, $P = 0.02$), *post-hoc* tests indicated no significant differences among treatments. When comparing between years in each treatment, mean fruit set in the DIUR_{TRT} differed significantly between 2013 (23.3%) and 2014 (0.0%) ($U_{17} = 80.0$, $P = 0.0008$; Fig. 2a), but not in the other three exclusion treatments.

A total of 144 whole fruits were collected in 2013 (55 from DIUR_{TRT}, 39 from NOCT_{TRT} and 50 from ALL_{TRT}), whereas only 15 whole fruits were collected in total during 2014 (10 from ALL_{TRT} and five from NOCT_{TRT}), due to fire, fruit predation and the overall low fruit production in the DIUR_{TRT}. Seed set

(average seed fruit⁻¹) differed significantly between the NOVIS_{TRT} and both the ALL_{TRT} and DIUR_{TRT} in 2013 ($H_{3,44} = 25.64$, $P < 0.0001$), but not among treatments in 2014 ($H_{3,24} = 4.12$, $P = 0.59$; Fig. 2b). Seed set in the DIUR_{TRT} in 2014 was zero (no fruit produced), a significant decrease from 2013 (42.6 ± 4.3 seed fruit⁻¹; $U_{17} = 80.5$, $P = 0.001$). Seed set differed significantly between years in the ALL_{TRT} (from 43.35 ± 6.1 in 2013 to 11.0 ± 7.2 seed fruit⁻¹ in 2014; $U_{17} = 75.0$, $P = 0.01$; Fig. 2b). In both years, minimal fruit appeared to be parasitised by wasps (or other insect species), and the effect that the parasites may have had on seed set and reproductive output was not considered further.

Total seed production differed significantly between the NOVIS_{TRT} (0 seed plant⁻¹) and both the DIUR_{TRT} (2433 ± 457 seed plant⁻¹) and the ALL_{TRT} (2129 ± 424 seed plant⁻¹) in 2013, but there was no significant difference in total seed produced in the same treatments in 2014 ($H_{3,24} = 3.61$, $P = 0.31$; Table 3). Significantly more seed was produced per plant in the DIUR_{TRT} in 2013 (2433 ± 457 seed plant⁻¹) than in 2014 (0 seed plant⁻¹; $U_{17} = 57.5$, $P = 0.004$; Fig. 2c). Seed flower⁻¹ differed significantly between the NOVIS_{TRT} (0 seed flower⁻¹) and both the NOCT_{TRT} (10.39 ± 2.02 seeds flower⁻¹) and ALL_{TRT} (10.03 ± 1.99 seed flower⁻¹) in 2013 ($H_{3,44} = 24.31$, $P < 0.001$), but did not differ among treatments in 2014 ($H_{3,21} = 3.61$, $P = 0.31$; Fig. 2d; Table 3). Between years, seed flower⁻¹ decreased significantly in the NOCT_{TRT} ($U_{16} = 66.5$, $P = 0.004$) and the DIUR_{TRT} ($U_{15} = 50$, $P = 0.026$; Fig. 2d, Table 3).

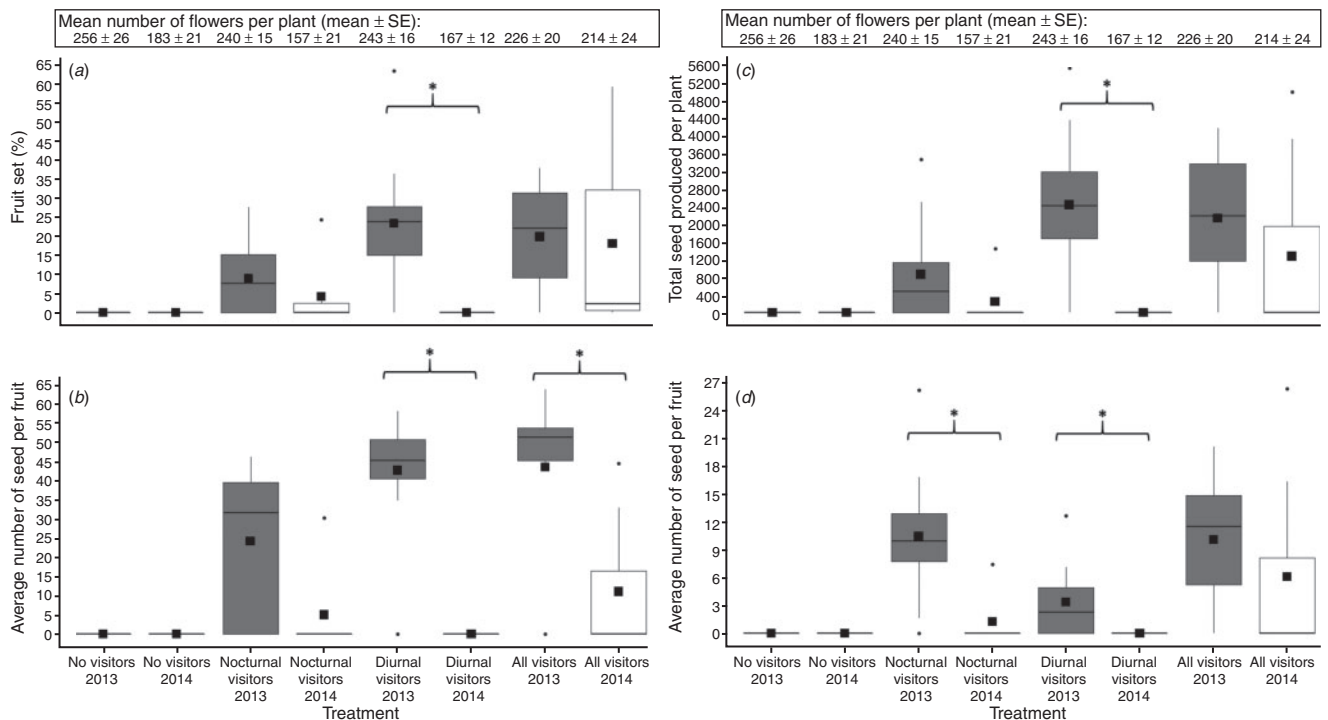


Fig. 2. Reproductive output of *Aloe peglerae* plants in pollinator selective exclusion treatments in two flowering seasons. 2013 (grey boxes) represents a 'good' flowering year and 2014 (white boxes) represents a 'poor' flowering year. (a) Fruit set (proportion of flowers that set fruit); (b) average number of seed per fruit (seed set); (c) total seed produced per plant; (d) average seeds per flower (2013: $n = 12$ plants treatment⁻¹; 2014: $n = 7$ plants in 'no visitors' treatment and 'all visitors' treatment six plants in 'nocturnal visitors' treatment and five plants in 'diurnal visitors' treatment). Thick solid lines represent medians, solid squares represent means, outer edges of boxes represent interquartile-ranges, vertical bars represent minimum and maximum values and solid dots represent outliers. Treatments significantly different between years are indicated: * $P < 0.05$.

Germination trials and seed viability

Germination began to slow 10 days after commencing the trials in both years, with the final seed germinating after 19 days in 2013, and 18 days in 2014. Cumulative germination, MGT and total viability results in 2013 and 2014 for each treatment were combined, due to low sample sizes in 2014, for statistical analyses. Cumulative percentage germination and other results for individual treatments in each year are presented in Supplementary material table S4. The cumulative percentage germination did not differ among treatments (90–97%; $H_{2,29} = 4.25, P = 0.12$). Similarly, MGT showed no significant difference between treatments (range: 6–9 days; $H_{2,29} = 2.15, P = 0.14$). Total seed viability (germinated seeds plus viable seeds after tetrazolium) was not significantly different between treatments ($H_{2,29} = 5.66, P = 0.06$), ranging from 90 to 98%. Total viability did not show any significant difference between years in the ALL_{TRT} and the NOCT_{TRT} ($\chi^2_1 = 0.60, P = 0.44$ and $\chi^2_1 = 1.94, P = 0.16$ respectively).

Discussion

Effects of variable flowering on bird (mobile) pollinators

Reproductive output of *A. peglerae* decreased between years, and most noticeably for the DIUR_{TRT}, where birds were regular visitors. Although the lower reproductive success in the poor flowering year may be linked to the fewer visits by primary pollinators attracted to the limited nectar supply (fewer flowering plants), we cannot exclude the possibility that poorer overall plant condition played a role in reduced reproductive output. The decrease in bird visitation rates during the poor flowering year suggests a disproportionate decrease in bird abundance, and that the generalist nectar-feeding birds may avoid the site entirely when resources become too low (and dispersed). Because of their vagility, birds are able to easily respond to available resources (e.g. MacNally 1996; Malizia 2001; Kuiper *et al.* 2015), optimising foraging in a way that is different to less mobile non-flying small mammals. The lower flowering proportions in the subpopulation and the smaller inflorescences (fewer flowers), suggest that foraging on this nectar source during a poor flowering year could be uneconomical, and it may be more beneficial to search for richer food sources elsewhere, rather than the same birds feeding on fewer plants more often. Opportunistic and/or migrant nectar feeders do not rely on predictable nectar resources and feed on nectar when it is abundant, and other food resources are not (e.g. Brown and Hopkins 1996; Franklin 1999). Therefore, visitation and feeding by such birds should decrease in poorer flowering years. The decrease in overall visitation rates between years suggests that nectar-feeding may be opportunistic and that the Cape rock-thrush, a winter altitudinal migrant (Johnson and Maclean 1994), uses nectar purely as an energy supplement during resource depleted winters. Indeed, the implied reduction in bird numbers during the poor flowering year suggests that more energetically viable resources are available elsewhere. The transient nature of the birds, and the likelihood of resource tracking, is further reinforced by the lack of recapture of birds ringed in two different flowering seasons (2012 and 2014), where only one male Cape rock-thrush, ringed in 2014, returned to the site only twice within the same flowering season (Payne *et al.* 2016).

Effects of variable flowering on small mammal (sedentary) pollinators

Small mammal visitation remained the same between years, implying that the small mammals, restricted by their limited mobility, are forced to exploit the resources available in their immediate surroundings. The Namaqua rock mouse and the sengi are both restricted to small home ranges (e.g. eastern rock sengi (*Elephantulus myurus*) males have home ranges of $\pm 3958 \text{ m}^2$; Ribble and Perrin 2005), and, therefore, are restricted to small foraging areas. Resources may be limited in the poor flowering year, resulting in the visitation rates remaining the same or increasing, as small mammals visit the plants more often to optimise the reduced available resources. Since different plants were assigned to the ALL_{TRT} in each year, the increased small mammal visitation in the ALL_{TRT} is likely due to the mobility and territoriality of the small mammals surrounding the individual plants sampled. However, the distance travelled by small mammals between flowering aloes, along with population density fluctuations, requires further investigation.

Competition for nectar between birds and small mammals

Although small mammal territories surrounding sampled plants likely differed between years, possibly contributing to the changes in small mammal visitation rates between years, sampling different territories within the Conservancy should not affect bird visitation, as birds are able to easily move between plants. Therefore, the decrease in bird visitation can be attributed to factors different than those which affect small mammals, the most likely being the availability of nectar resources. It is likely that there is competition between birds and small mammals for nectar resources. This is evident as more birds may be foraging during dusk and dawn for accumulated nectar produced by NOCT_{TRT} plants during sunrise (before cage changeovers) or sunset (after cage changeovers) in a poor flowering year. Approximately 67% of visits in the NOCT_{TRT} were made by birds (although this was not a significant change between years and had no effect on reproductive output after corrections), and these birds are probably depleting nectar resources available for small mammals. While birds are able to move to another area in search of other viable food resources, small mammals are forced to make use of the limited nectar available in their immediate surroundings. To meet energy requirements, small mammals need to: (i) find alternative plants at which to forage, (ii) forage at the same plants more often, and/or (iii) feed at the same plant throughout the night as nectar supplies become replenished. Camera trap footage shows *A. peglerae* flowers opening consistently throughout the night, as with *A. marlothii* (Symes and Nicolson 2008). *Aloe peglerae* nectar is consistently produced over a 24-h period, with nectar concentration remaining unchanged over time (S. L. Payne, unpubl. data), providing ample, good quality nectar for small mammals during the night and, where unconsumed by small mammals, for birds during the early hours of the morning.

Effects of variable flowering and subsequent pollinator visitation on reproductive output

The decrease in reproductive output between years further emphasises the primary role that birds play in the pollination

of *Aloe peglerae*. In the poor flowering year, no fruit was produced in plants pollinated only by birds, whereas plants pollinated by birds or small mammals produced minimal fruit. Plants that received no visits in both years (NOVIS_{TRT}) produced no fruit, suggesting that the aloe is reliant on a biotic pollen vector. Small mammals may be acting as alternative, albeit less effective pollinators (especially since they are less effective at moving pollen across greater distances, and between populations; Cunningham 1991), whereas the birds are moving to areas with more abundant food and water resources. Also, smaller floral displays in 2014 likely decreased the attractiveness of the area to potential pollinators (particularly birds) which subsequently lowered visitation rates and reproductive output (Sutherland 1986; Broyles and Wyatt 1990). Although small mammals can be destructive when removing flowers, often to the point where the plant does not produce fruit, the similar quality of seed produced by bird- and small mammal-pollinated plants suggests that small mammals are cross-pollinating to some extent, and further reinforces the suitability of the small mammals as alternative pollinators, in both 'good' and 'poor' flowering years (Payne *et al.* 2016). In both years, fruit showed evidence of frugivory (ALL_{TRT}: 35.2 and 92.0% of fruit produced in 2013 and 2014 respectively), although it is not known whether small mammals or birds (presumably the streaky-headed seed-eater) were feeding on the fruit, as no camera traps were active in the period between flowering and fruit harvest. Nevertheless, the increase in frugivory in the 'poor' flowering season (100% of fruit on some plants showed evidence of frugivory), could be an indication of limited food resources for animals, both per plant and across the entire flowering/fruitlet subpopulation, in the Conservancy.

The significant decrease in the number of flowers produced by plants in 2014 decreases the number of flowers available for pollination and fertilisation, which could be resulting in a lower fruit set, as well as lowering the amount of nectar available for pollinators. Small mammals are less efficient at cross-pollination (Faegri and van der Pijl 1979; Cunningham 1991). Consequently, they are likely, to some degree, to contribute to self-pollination on individual inflorescences. Since *A. peglerae* appears to be self-incompatible (Arena *et al.* 2013; Payne *et al.* 2016), transfer of genetically similar pollen by small mammals (and possibly birds as well) may be initiating the self-incompatibility reaction, decreasing reproductive output (e.g. Sutherland and Delph 1984).

Conclusion

Nectar is an important winter food source for birds and mammals alike (e.g. Symes *et al.* 2008, 2011; Schmid *et al.* 2015; Steenhuisen *et al.* 2015). A decrease in the proportion of flowering *A. peglerae* plants and subsequent decline in nectar availability may force vagile birds to avoid the site in search of more energetically viable resources. This was suggested by the decrease in visitation to, and reproductive output of, plants in the DIUR_{TRT}. Meanwhile, visitation by small mammals remained the same in the NOCT_{TRT}, but increased in the ALL_{TRT}, with reproductive output unaffected between years. This is most likely due to the limited mobility and home ranges of the small

mammals, where they are forced to exploit and compete for resources available in their immediate environments.

Along with decreased visitation rates, minimal fruit production could also be as a result of limited resources available to the plants (especially maternal resources), and climatic conditions before flowering, all of which require further investigation. Since an alternative pollinator appears to adequately pollinate the species, this – along with the perennial nature of the plant – may also buffer the species against years of low seed production in poorer flowering years, with low pollinator abundance. *A. peglerae* may be viable in small subpopulations and protected from Allee effects, which could further decrease reproductive output, especially if the primary pollinator is absent from the area. However, the conservation of this endangered and endemic aloe should be prioritised, as the variation in flowering could be detrimental to the persistence of *A. peglerae*, notwithstanding the current effects of anthropogenic disturbance on this species.

Conflicts of interest

The authors declare no conflicts of interest.

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