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Coexistence of succulent tree aloes: partitioning of bird pollinators by floral traits and flowering phenology

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Coexistence among species that lack genetic barriers to hybridization usually depends on pre-mating isolating barriers. It has been difficult to explain coexistence among African *Aloe* species because they readily hybridize, often flower simultaneously and are mostly bird-pollinated. Here we show that co-flowering aloes in a succulent thicket community in South Africa partition the fauna of flower-visiting birds. *Aloe* species with small amounts of concentrated nectar in long corolla tubes were pollinated primarily by long-billed sunbirds. These species co-flowered with species with large amounts of dilute nectar in short corolla tubes which were pollinated primarily by short-billed, generalist nectarivores. *Aloe* species which share pollinators tend to have divergent flowering times and differences in pollen placement on birds. Without these isolating barriers, genetic dissolution of sympatric *Aloe* species would be likely.

The extent to which pollination plays a role in structuring plant communities in terms of species composition and functional traits is still poorly understood. Plants may interact positively by facilitating each other's pollination (Gross et al. 2000, Bruno et al. 2003, Moeller 2004), or negatively through either competition for pollinator services (Levin and Anderson 1970) or production of unfit hybrids (Arnold and Hodges 1995). These interactions may influence trait evolution or sorting of species into assemblages according to existing traits such as flowering time (Stiles 1975, 1977), floral morphology that influences pollen placement (Brown and Kodric-Brown 1979, Armbruster et al. 1994), divergence in time of pollen availability (Stone et al. 1998), and nectar and scent properties that filter flower visitors (Bruneau 1997, Johnson et al. 2006, Salzmann et al. 2006).

It has been difficult to explain the coexistence of *Aloe* species because they hybridize readily (Reynolds 1969, Barker et al. 1996, de Wet 2004), yet often co-flower en-masse and share a floral syndrome consistent with bird pollination. Most authors have considered sunbirds to be the primary pollinators of aloes (Skead 1967, Hoffman 1988, Ratsirarson 1995, Stokes and Yeaton 1995). However, there is also evidence that some *Aloe* species are visited mainly by short-billed generalist birds (Oatley and Skead 1972, Johnson et al. 2006). Hence, one solution to the problem of *Aloe* species co-existence would be if there is a greater diversity of bird pollination systems in the genus than was previously imagined. In the bird-pollinated pantropical genus *Erythrina*, for example, co-occurring species are often pollinated either by specialist nectarivores (hummingbirds in Americas and sunbirds in Africa) or generalist occasional nectarivore birds (Guillarmod et al. 1979, Bruneau 1997). Similarly in *Heliconia*, coexisting species partition hummingbirds according to their bill shapes (curvature and length) and territoriality (Stiles 1975). To determine whether there is indeed more than one bird pollination system in *Aloe*, we took the approach of studying several *Aloe* species in a single natural community, such that any differences in bird visitors among the aloes would reflect actual foraging choices by birds and not simply the composition of the local bird assemblage. We identified a guild of five co-flowering 'ornithophilous' *Aloe* species that co-exist in dense succulent thicket habitat in South Africa as being suitable for this purpose.

Our aim in this study was to document the flowering phenology, floral traits and pollinators of sympatric 'ornithophilous' *Aloe* species. We addressed the following questions: 1) Do co-flowering species partition bird pollinators? 2) Do *Aloe* species that share bird pollinators show divergence in flowering time or place pollen on different sites on these birds? 3) Is there an association between the floral morphology and nectar properties of *Aloe* species and their bird visitors?

Methods

Study area and species

This study was conducted in the Gamtoos River Valley (33°50′S, 24°55′E) in southeast South Africa. The

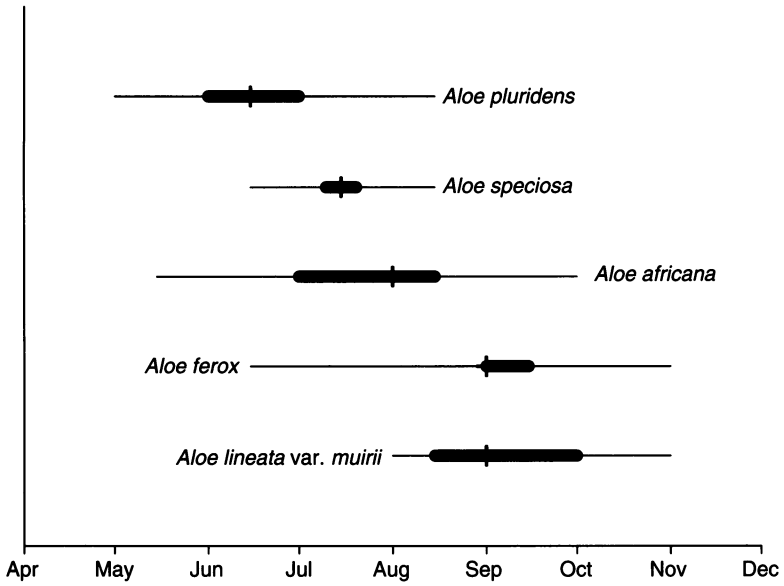

Fig. 1. Mean valley-wide flowering phenology from 15 sites over a two year period for the five most common aloes in the Gamtoos River Valley. Thin lines indicate total flowering time (at least one plant in flower), thick lines indicate peak flowering period (50% of plants in flower), and vertical lines indicate the time when the maximum number of individuals were in flower.

Gamtoos River Valley is bordered to the south by the Indian Ocean and to the northwest by the Baviaanskloof World Heritage Site. This semi-arid area falls within the transition zone between summer and winter rainfall regimes: most of the ca 430 mm annual rain falls in the spring and autumn. Temperatures are mild in winter when they seldom drop below 10°C, and warm in summer, when they may exceed 40°C. Members of the Aloaceae are keystone elements in the thicket ecosystems of southeastern South Africa, and notably so in Gamtoos Valley Thicket (Vlok et al. 2003).

At the study site, extensive populations (tens of thousands of individuals) of the single stemmed aloes (sensu Van Wyk and Smith 2003) *Aloe pluridens*, *A. speciosa*, *A. africana*, *A. ferox* and *A. lineata* var. *muirii* coexist within the same thicket habitat. These species have few genetic barriers to hybridization with each other, as evidenced by the results of controlled interspecific pollination experiments and the existence of occasional natural hybrids between species with overlapping flowering periods (Botes et al. unpubl.). Reynolds (1969) places the study species into five taxonomic sections, but the precise phylogenetic relations of these *Aloe* species have not yet been established. All five species are self-incompatible and thus dependent on pollinators for seed production (Botes et al. unpubl.). In addition to birds, honeybees frequently visit *Aloe* flowers for the purpose of gathering pollen and nectar. However, experiments in which birds, but not insects, were excluded from inflorescences of the five study species showed that bees make only small, and in some cases negligible, contributions to seed production (Botes et al. unpubl.). We selected 15 sites for observation along the length of the valley from the coast near the Gamtoos River mouth to ~30 km inland; five monospecific stands, and ten sites with two or more species in combination.

Flowering phenology

Because of the impenetrable nature of the thicket vegetation and steep terrain, we used a medium strength spotting scope (20–40 × magnification) to record the flowering phenology. We thus recorded the state of all the inflorescences on 60 randomly spotted individuals per species present at each of the 15 sites every 15 days for the duration of the 2004 and 2005 flowering seasons. We scored individual inflorescences according to the following six states of flowering: pre-anthesis (state 0), flowering commencing (state 1), flowering bottom half of inflorescence (state 2), flowering top half of inflorescence (state 3), flowering ending and mostly fruiting (state 4), and flowering complete (state 5). These flowering states were used to assess the degree of synchronicity within and between sites for individual species. Flowering was defined as the point of anthesis where the first anthers protrude from the perianth tube. The peak flowering period for an individual species was defined as the time period when more than 50% of the individuals that were to flower during the season, flowered. Flowering times in 2004 and 2005 were compared using a paired t-test. To determine if flowering times of the study species are influenced by the presence of congenerics, we used a paired t-test to compare the mean flowering times of the species between monospecific and mixed plots for both the 2004 and 2005 data. We analysed the phenological data for aggregation, random or staggered pattern using the null model described by Poole and Rathcke (1979) and modified by Williams (1995).

Floral ontogeny and morphology

Floral development was investigated in ten individuals of each species. We especially focused on the final presentation of the individual flowers to the pollinator at anthesis, and the positional nature of the anthers and stigma.

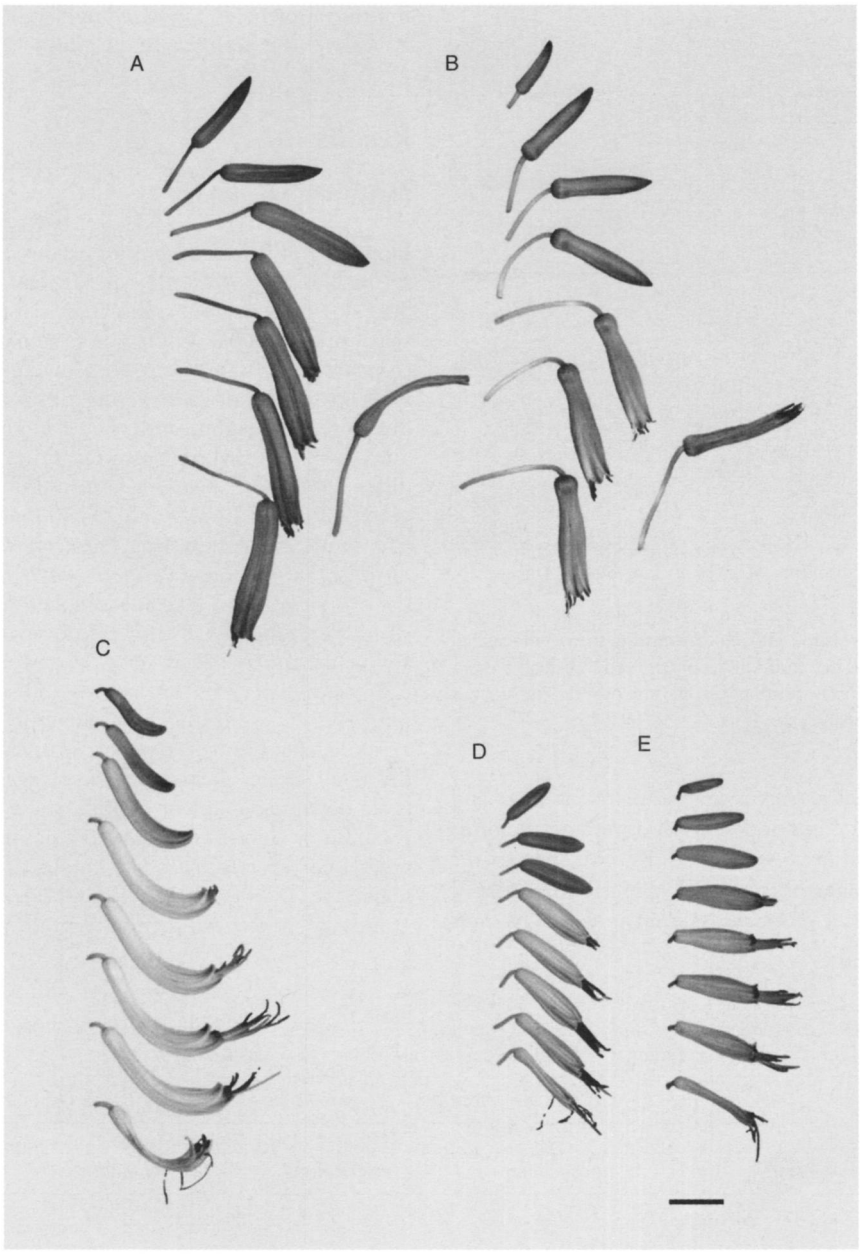

Fig. 2. Comparative floral development for the three floral groups, with representative flowers from the different stages – male phase (anthesis) at the fifth-sixth flower from the top, female phase at the sixth-seventh flower. Clockwise from top left: group 1 – (A) *A. pluridens*, (B) *A. lineata* var. *muirii*; group 2 – (D) *A. speciosa*, and (E) *A. ferox*; and group 3 – (C) *A. africana*. Scale bar = 15 mm.

Nectar

The volume of nectar in ten newly opened flowers from each of twelve plants per species was measured in situ at one locality, using calibrated 100 ul micropipettes. Nectar sugar concentration was quantified with a temperature-compensated, handheld nectar refractometer. Racemes were bagged prior to anthesis with fine mesh pollination bags to exclude floral visitors. Nectar data were analyzed by first obtaining mean values for individual plants, and then using these as replicates to compare mean values among species using oneway ANOVA (the data were normally distributed), followed by the Tukey pairwise multiple comparison test.

Bird pollinators, feeding positions and pollen deposition sites

Bird visitors to each species were recorded while working within the various sites. Formal observations were made using a medium strength spotting scope (20–40 × magnification), within both mixed and pure stands, for 15 min every hour on one day at a stationary position. We also walked along game paths through the vegetation for a distance between 300–400 m at two of the larger mixed sites where all species were present. Each transect was walked for 10 min every hour between sunrise and sunset on one day during peak flowering of each species. We recorded the identity and feeding habit of the bird visitors,

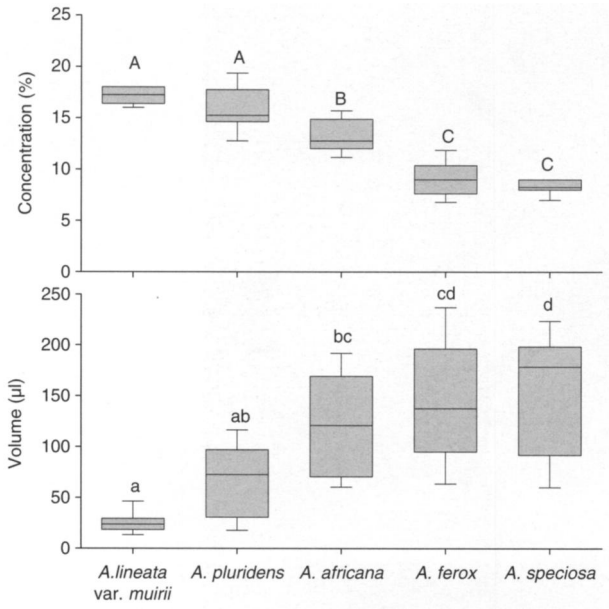

Fig. 3. Mean nectar volume and concentration from ten bagged flowers from each of twelve individuals per species. Vertical bars = SE of the mean (±SE). Similar letters denote no significant differences between means.

with special attention given to whether or not anthers and stigma were touched. Sites of pollen deposition on the birds were easy to establish because of the distinctive color of the densely deposited pollen of co-flowering species (in order of flowering sequence: *A. pluridens*: salmon pink; *A. speciosa*: mustard brown; *A. africana*: bright yellow; *A. ferox*: orange; *A. lineata* var. *muirii*: salmon pink).

Results

Flowering phenology

Flowering of the study species occurred during the winter–spring flowering season from May to November (Fig. 1). The flowering season commenced at the same time each year, but the 2005 season was terminated a month earlier compared to the previous year, owing to a prolonged dry spell. However, peak flowering times of the study species did not differ significantly between these two years ($t = 1.63$, $p = 0.18$). Mean flowering times for species did not differ significantly between pure and mixed stands in either year (2004: $t = 1.43$, $p = 0.23$; 2005: $t = 2.01$, $p = 0.11$). The sequence of flowering (*Aloe pluridens, A. speciosa, A. africana, A. ferox, A. lineata* var. *muirii*) was the same over the two-year period. Overall, a higher median proportion of *A. pluridens* individuals flowered over the two seasons than any of the other species (*A. pluridens* – 65%; *A. africana* – 35%; *A. speciosa* – 35%; *A. ferox* – 30%; and *A. lineata* var. *muirii* – 26%). If the physiologically possible flowering season is taken to be the period spanned by flowering of all the study species then significant staggering was evident for peak flowering dates of all five study species ($V = 0.001$ $p < 0.003$). Flowering patterns of the three specialist-pollinated species showed an even higher degree of staggering ($V = 0.0001$, $p < 0.001$). Flowering in either groups of species is neither significantly staggered nor

Table 1. List of recorded independent observations of bird visitation to the five aloes, differentiated into their different visitation actions; where P = legitimate pollinator, CP = coincidental pollinator, NR = nectar robber, DF = destructive forager.

	A. pluridens		*A. lineata var. muirii*		*A. africana*		*A. speciosa*		*A. ferox*	
Species	No. observations	Action	No. observations	Action	No. observations	Action	No. observations	Action	No. observations	Action
Malachite sunbird (*Nectarinia farmosa*)	22	P	4	P	6	P	9	NR	105	NR
Greater double-collared sunbird (*Cinnyris afra*)	76	P	74	P	75	P	26	NR	54	NR
Amethyst sunbird (*Chalcomitra amethystina*)	113	P	1	P	37	P	11	NR	5	NR
Collared sunbird (*Hedydipna collaris*)	4	NR			1	NR			4	NR/CP
Weaver (*Ploceus* spp.)	10	NR/CP			34	NR/CP	121	P	344	P
Speckled mousebird (*Colius striatus*)							32	P	101	P
Red-winged starling (*Onychognathus morio*)							14	P	15	P
Cape white-eye (*Zosterops pallidus*)							12	P	5	P
Sombre bulbul (*Andropadus importunus*)			2	DF			2	P		
Forked-tailed drongo (*Dicrurus adsimilis*)							8	CP	3	CP
Cape rock thrush (*Monticola rupestris*)									2	CP
Dusky flycatcher (*Muscicapa adusta*)									1	CP
Streaky-headed canary (*Serinus gularis*)					2	DF	15	DF	3	DF

Fig. 4. Feeding positions showing main pollinator: (A) female amethyst sunbird on *A. pluridens*, (B) male greater double-collared sunbird on *A. lineata* var. *muirii*; (C) male greater double-collared sunbird on *A. africana*; and (D) yellow weaver on *A. ferox*, (E) a Cape weaver on *A. speciosa*.

aggregated if the physiologically possible flowering season is taken to include the whole year (*Aloe* species can be found in flower at any month of the year in South Africa).

Floral ontogeny and morphology

Flowers of these five *Aloe* species were all protandrous and they matured acropetally on the inflorescence racemes. Flowers on the northern (sunny) side of the racemes opened earlier than those on the shaded side. The five species converged into three clear floral groups based on their floral morphology, development, and final presentation to the pollinators. Group 1 consisted of *Aloe pluridens* and *A. lineata* var. *muirii*. Both species have long-tubular flowers that hang downward on elongated pedicles at anthesis, having dropped downward from the flower bud's upright position prior to anthesis (Fig. 2A–B). Flowers of these two species lift against the raceme axis after successful pollination, only to drop down again at fruit maturation. The adpressed filaments and style are partially exserted, with the anthers facing inward at the mouth of the perianth tube. Group 2 consisted out of *A. speciosa* and *A. ferox*. These two species have short-tubular, actinomorphic flowers with short pedicles (Fig. 2D–E). Flowers are presented nearly horizontally for the duration of their development. At anthesis, the exerted filaments fully block the opening of the tapering perianth tube. The anthers face inward towards the floral axis (facing each other). *Aloe africana* (group 3) was unique in relation to the other species because of its long fused perianth tube that is strongly curved (almost a right angle) at anthesis (Fig. 2C). Flowers are carried on short pedicels, and hang downward throughout their developmental stages, giving the individual racemes a sharp conical shape. The exerted filaments are presented slightly upward from the hanging position of the flower, with all the anthers facing up. The filaments fully block the tapering entrance to the perianth tube. Typically, flowers of all five species lasted three to four days after anthesis.

Nectar

There were significant differences in nectar volume ($F = 15.34$, $p < 0.001$) and concentration ($F = 77.87$, $p < 0.001$) among the five species (Fig. 3). The nectar properties showed a strong association with floral morphological traits. The long-tubed species, *Aloe pluridens* and *A. lineata* var. *muirii* (group 1), produced nectar in lower volumes and higher sugar concentrations that did the short-tubed species, *A. speciosa* and *A. ferox* (group 2). Nectar of *A. africana* (group 3) was intermediate between these two groups. In *A. pluridens*, *A. lineata* var. *muirii*, and *A. africana*, the nectar was located at the base of the perianth. Nectar in *A. speciosa* and *A. ferox* was produced in such large quantities that it filled the perianth tube and was pushed in amongst the tight exerted filaments where hydrostatic forces prevented it from flowing out.

Bird pollinators, feeding positions and pollen deposition sites

In terms of bird visitors, the five species could be readily categorized into the same three groups established above. *Aloe pluridens* and *A. lineata* var. *muirii* were visited almost exclusively by long-billed nectarivorous sunbirds (Table 1). Sunbird visitors to these species perched on the inflorescence peduncle below the raceme from where they foraged at all the basal, open flowers by extending their heads upward (Fig. 4A–B). Pollen of both species was deposited on the underside of the mandible and chin (Fig. 5) as the bird slid its beak over the inward facing anthers in the entrance of the perianth tube.

Flowers of *A. africana* were visited principally by sunbirds which fed from an upside down position (Fig. 4C). Because of the curved nature of the flower, birds were only able to probe successfully, and hence reach the nectar at the base of the perianth, from this upside-down position. This resulted in the accurate placement of pollen only on the crown of the bird's head in this species (Fig. 5).

Aloe speciosa and *A. ferox* were visited by a range of short-billed occasional nectarivores (eight species), with weavers being the most frequent (Table 1). Birds probed in two ways: (1) after landing on the leaf rosette, they probed open flowers near the bottom of the inflorescence or climbed on below the advancing front of acropetally maturing flowers (Fig. 4D); and (2) after landing on the top of the sturdy inflorescence they climbed down to the advancing front of maturing flowers and probed upside down (Fig. 4E). In both cases, birds probed right through the exserted filaments, and because the anthers faced each other toward the floral axis, pollen was deposited in a mask-like fashion on the bird's face (Fig. 5A). Mousebirds (the only non-passerine bird to visit these aloes), also had pollen smeared on their breasts and underbellies (Fig. 5B) as they climbed awkwardly over the inflorescences.

Several other bird species were visitors to the five study species, but did not seemingly play an important role in their pollination. This was because their feeding behavior was either not conducive to consistent stigma contact (e.g. short-billed collared sunbirds) or because they were not targeting the aloes as such, but the bees that were active on the flowers (e.g. forked-tailed drongo and dusky flycatcher) or because they fed destructively on the flowers (e.g. streaky-headed canary).

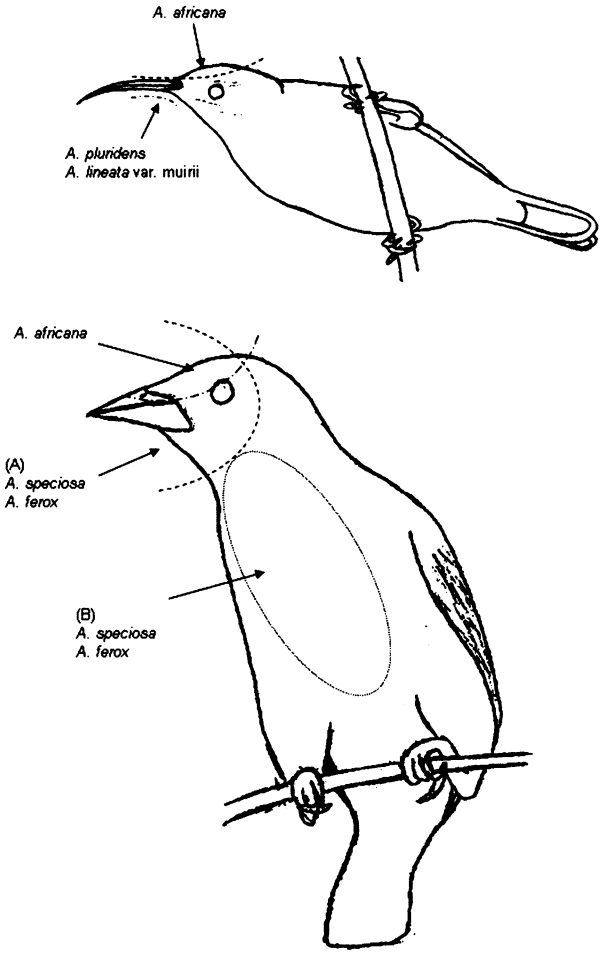

Fig. 5. Pollen deposition sites (redrawn from photos) on the two classes of avian pollinators. Top: nectarivore sunbird feeding at *A. africana*, *A. pluridens* and *A. lineata* var. *muirii*. Bottom: occasional nectarivore weaver feeding at *A. speciosa*, *A. ferox*, and occasionally at *A. africana*. (A) denotes the main pollen deposition site on occasional nectarivores, with (B) indicating the additional site, mainly for mousebirds, when feeding at these two aloes.

Discussion

This study shows that at least two distinct bird pollination systems occur in ornithophilous *Aloe* species. The first, involving specialist long-billed sunbirds as pollinators, is associated with long-tubed flowers with small volumes of relatively concentrated nectar (*A. pluridens*, *A. lineatea* var. *muirii*, *A. africana*), and the second, involving short-billed occasional nectarivores as pollinators, is associated with short-tubed flowers with large volumes of relatively dilute nectar (*A. ferox*, *A. speciosa*).

The dichotomy in nectar volume and concentration between flowers pollinated by specialist and occasional avian nectarivores appears to be a widespread pattern among both old and new world plants (Johnson and Nicolson 2008).

Although it has been shown that nectar sugar composition varies among bird pollination systems in American *Erythrina* (Baker and Baker 1983) this does not apply to the African aloes where all species have hexose-dominated nectar (Van Wyk et al. 1993). In *Aloe*, partitioning of specialized and generalist nectarivorous birds through nectar can thus only involve its sugar concentration and volume. Sunbirds just like hummingbirds are known to prefer concentrated nectar (Hainsworth and Wolf 1976, Lloyd 1989), which might explain the relatively concentrated nectar found in sunbird-pollinated aloes, but it is not yet clear whether the highly dilute nectar in aloes pollinated by generalist birds is an outcome of selection through foraging preferences by these birds or, alternatively, a filter that reduces visitation by ineffective pollinators, such as long-billed sunbirds and bees (Johnson et al. 2006). *Aloe africana* has intermediate nectar traits and is visited by both guilds of birds. However, the flowers of *A. africana* are morphologically most suitable for sunbird pollination (long fused perianth tube that is curved to match sunbird bills) and are destroyed when foraged on by short-billed generalist weaver birds.

The flowering patterns of the five *Aloe* species were significantly staggered within the observed flowering period. This is even more evident for the three specialist nectarivore-pollinated species which are potential competitors (limited sample size precluded this analysis being performed for the two species with generalist bird pollination systems). Our conclusion that flowering times are staggered is based on an analysis which assumes that the flowering periods of aloes in our study area are generally constrained to the winter months. Although other *Aloe* species can be found in flower at any time of the year in South Africa (Reynolds 1969), *Aloe* species in succulent thicket vegetation invariably flower only in the winter months. The basis for winter-flowering of aloes in succulent thicket is not fully understood, but probably relates to greater nectar requirements of birds during a period which is both cool and characterized by a shortage of alternative food sources such as insects and fruits. Another possibility is that bird density in succulent thicket increases during winter because of migration of birds from colder inland habitats into the coastal river valleys. Selection would favour flowering times in *Aloe* species that enable them to exploit periods when birds experience nectar shortages, with the net result that flowering becomes staggered in the community and birds obtain a continuous supply of nectar in the winter. From the perspective of encouraging bird residency, therefore, the interactions among *Aloe* species may be facilitative (Feinsinger 1978).

It may be coincidental that aloes with different pollination systems tended to co-flower, while those with similar pollination systems tended to flower sequentially (Fig. 1). However, a good case could also be made for local adaptation or ecological species sorting (Rice and Pfennig 2007), as the effects of these flowering patterns are to minimize ecological overlap between those species that share pollen placement sites on the same pollinators. Conversely, co-flowering appears to be possible for species that differ in pollinators or have different pollen placement sites on shared pollinators. *Aloe africana* was unique among the study aloes because of its unusual placement of pollen on the crown of birds. Nevertheless, the prolonged flowering of *A. africana*, and its sharing of pollinators with other *Aloe* species, increases its risk of forming hybrids. In particular, pollen transfer to and from both *A. ferox* and *A. speciosa* via weavers is quite possible due to the partial overlap in pollen deposition, and plants of hybrid origin have been found where *A. africana* grows intermingled with either of these two aloes (Botes et al. unpubl.).

Conclusions

Co-flowering ornithophilous aloes effectively partition the bird pollinator community through differences in floral morphology and nectar traits, while species that share bird pollinators tend to flower sequentially or utilize different pollen placement sites on the same birds. Given the lack of genetic barriers to hybridization in aloes it is likely that these differences in pollination systems and flowering phenology enable a greater number of *Aloe* species to coexist than would otherwise be possible. Indeed the number of co-flowering species in the assemblage we studied is rare elsewhere, and only occurs in the few hotspots of aloe diversification (Reynolds 1969, Holland 1978). Thus, it is concluded that studies of pollination systems are likely to contribute to our understanding of the maintenance of species richness in plant communities.

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