

## The pollination ecology of *Aloe ferox* Mill.

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The breeding system and pollination ecology of *Aloe ferox* Mill. were investigated. The relationship between plant height, raceme number, raceme length and percentage fruit success was determined for 93 plants. There was a significant positive relationship between plant height and raceme number but the percentage fruit success did not increase with an increase in plant height, number of racemes and mean and total raceme length. A description of post-anthesis flower development is given. Optimal stigma receptivity occurs 8 to 24 h after anthesis and is synchronized with maximum nectar concentration and volume. The flower morphology of this species suggests a bird-pollinated syndrome. This study shows, however, that African honey bees may also play a role in its pollination. Bees visit the anthers as soon as they are exerted beyond the floral tube and, because the stigmas are at least partially receptive at this early post-anthesis stage, fertilization can be affected. This species is self-incompatible and selection pressures have probably been to minimize the number of flowers open on an inflorescence at any one time.

Die voortplantingswyse en bestuiwingsbiologie van *Aloe ferox* Mill. is ondersoek. Die verhouding tussen planthoogte, aantal trosse, tros lengte en persentasie vrugvorming is vir 93 plante bepaal. Daar was 'n betekenisvolle positiewe korrelasie tussen planthoogte en aantal trosse, maar die persentasie vrugvorming het nie vermeerder met 'n toename in planthoogte, die aantal trosse en die gemiddelde en totale tros lengte nie. 'n Beskrywing van blomontwikkeling na antese word gegee. Optimale stempelontvanklikheid kom van 8 tot 24 uur na antese voor en is met die maksimum nektarkonsentrasie en -volume gesinchroniseer. Die blomorfologie van hierdie spesie skep die indruk van voëlbestuiwing. Hierdie ondersoek het egter aangetoon dat Afrikaanse heuningbye ook 'n rol in bestuiwing mag speel. Bye besoek die blomme sodra die helmknoppe by die blombuis uitgestoot word en aangesien die stempels ten minste gedeeltelik ontvanklik op hierdie vroeë na-antese stadium is, kan bestuiwing beïnvloed word. Hierdie spesie is self-onverenigbaar en seleksiedruk het waarskynlik gelei tot 'n vermindering van die aantal oop blomme op 'n bloeiwyse op enige stadium.

**Keywords:** *Aloe*, breeding system, pollination, seed set, stigma receptivity

'But it cannot be said that aloes . . . are so dependent on sunbirds that if the birds were to be exterminated the aloes would fade from the scene with them. There are too many other pollinators . . . (and) . . . the value of birds as pollinators must be a mere bagatelle in the economy of aloe survival.'

(from Skead 1967)

'However, there is danger in assuming that the needs of only one kind of pollinator are catered to by the flower. An illustration would be a species of *Aloe* from South Africa. Red, scentless, broadly tubular flowers with exerted stamens and styles, a plentiful supply of only slightly viscous nectar at the base of the corolla tube, and a standing on the inflorescence for a nectar taker than will contact anthers and stigmas all add up to a sunbird pollination syndrome in Africa. But honey bees also visit these flowers (to collect pollen), and they must play some role in the pollination process too.'

(from Baker 1983)

### Introduction

With a range of over 900 km, *Aloe ferox* is widespread and common (Reynolds 1950). It occurs in a great variety of habitats, often at the ecotone between vegetation types.

To date, research on *Aloe* has focussed on popular guides (Jeppe 1969) and taxonomic works (Reynolds 1950) including cytogenetic (Brandham 1975; Riley & Majumdar 1979), and anatomical and phytochemical investigations (Beaumont *et al.* 1986; Reynolds 1986). Habitat descriptions (Holland *et al.* 1977) and studies on the effects of disturbance on *A. ferox* populations in the southern Cape (Holland & Fuggle 1982; Bond 1983) have also been

conducted. In addition, Holland (1978) has discussed the evolutionary biogeography of the genus.

Hybridization within the genus is common (Reynolds 1950), and has been known for almost a century (Riley & Majumdar 1979). It has probably played a role in the evolution of the tribe Aloineae (Riley & Majumdar 1979). Besides Vogel's (1954) and Skead's (1967) brief descriptions of bird pollination in the genus, I am unaware of any other published work on the pollination ecology of *Aloe*. Skead (1967) and Baker (1983) warn that pollination within the genus may be carried out by more than one pollinator guild. The orange-reddish *A. ferox* flowers, arranged on densely multiflowered, erect racemes, usually in a single inflorescence, suggest a bird-pollinator syndrome. However, as noted by Marloth (1915) and Baker (1983), bees also visit the flowers of most *Aloe* species to collect pollen and nectar and probably play some role in pollination as well.

By combining natural history observations with manipulative breeding experiments I suggest that in the self-incompatible flowers of *A. ferox* both insects and birds may act as pollinators and I show how this species has evolved to exploit both groups.

### Materials and Methods

#### Study sites

This study was conducted at two sites in Port Elizabeth. A population of 93 plants growing on a north-east facing slope in the Baakens River Valley at Fort Frederick (33°58'S, 25°37'E) was used for determining:

- Relationships between plant height and flower and fruit production;
- Floral development and morphology;
- Self-compatibility levels;
- Number of pollinators and frequencies of visits by *Apis*

*mellifera* (African honey bee).

Individuals growing in the University of Port Elizabeth gardens (34°00'S, 25°41'E) were used for determining:

- Nectar concentration and volume changes per flower over a three-day period;
- Controlled pollination experiments;
- The timing of stigma receptivity.

Both sites receive about 600 mm of rain per annum, and occur within a kilometre of the sea. The study was conducted from early July until late August 1986 when all plants had finished flowering.

#### Plant height vs. flower and fruit production

Plant height was measured from the apex of the newest leaf produced in the centre of the rosette of leaves, to the ground on the upward side of the slope.

The relationship between raceme length and flower number for 20 racemes from separate plants was determined. I used the resultant regression equation in subsequent tests of percentage fruit success. This was calculated as the number of fruits produced as a percentage of the number of flowers available. The number of fruits produced per raceme and percentage fruit success was measured. I regressed these measures against plant height and raceme length and number. The number of ovules per locule and seeds per capsule was determined from random samples.

#### Floral morphology and development

Changes in flower and stigma colour and shape were recorded. As the filaments lengthen the anthers are exerted beyond the floral tube. For the purposes of this study anthesis is defined as beginning when the first exerted anther is seen at the mouth of the floral tube.

Stigma receptivity was determined by cross-pollinating flowers at different times after anthesis. Fifteen flowers from each of two plants for each post-anthesis time period were used. The anthers were removed at anthesis. The stigmas received pollen:

- Two hours after anthesis. This was the time that the stigmas emerged from the floral tube and pollen transfer became possible;
- Eight hours after anthesis;
- One day after anthesis and every 24 h thereafter until five days after anthesis.

The racemes were bagged before and after pollination.

#### Nectar

Nectar production was measured with a calibrated micropipette. A hand refractometer was used to measure the refractive index of the nectar.

Nectar volume and concentration was measured in 10 flowers from a single plant at the bud stage (1 h prior to anthesis) and at 2, 8, 24, 48 and 72 h after anthesis. By staggering the starting time, all readings could be made at the same time on the same day. The inflorescences being used for this were enclosed in fine-mesh terylene netting bags which excluded even small insects.

#### Floral visitors

Floral visitors were observed for a total of 30 h on 10 different days in July 1986. Although I grouped visitors into pollinators, visitors and destructive foragers, I did not measure whether pollen transfer actually occurred. If I observed copious amounts of pollen on the feathers of birds and hairs of insects I classified such species as pollinators. Visitors without obvious pollen collections were classed as visitors only.

The number of visits by the African honey bee was

measured for 30 min each hour on one day (10h00–16h00). Ten flowers on one raceme were marked at anthesis and the number and duration of visits per flower by *Apis mellifera* were recorded. I also recorded their pollinator behaviour.

#### Breeding experiments

To determine the breeding system of *A. ferox* three treatments were performed and the resultant fruit set recorded.

- Four racemes (comprising 1 569 flowers) were bagged as a control;
- Flowers ( $n = 244$ ) from two different racemes were repeatedly pollinated (5–10 events per flower) with pollen from flowers on the same raceme (geitonogamy);
- Flowers ( $n = 212$ ) from two different racemes were repeatedly cross-pollinated with pollen from different plants.

I bagged the racemes containing the manipulated flowers before and after treatments.

#### Results

##### Plant height vs. flower and fruit production

Seedlings and plants less than 1 m high dominate the Fort Frederick population (Figure 1). Plants taller than 1 m make up less than 8% of the population (Figure 1).

Fifty-five of the 93 observed individuals flowered during the study. The shortest plant to produce an inflorescence

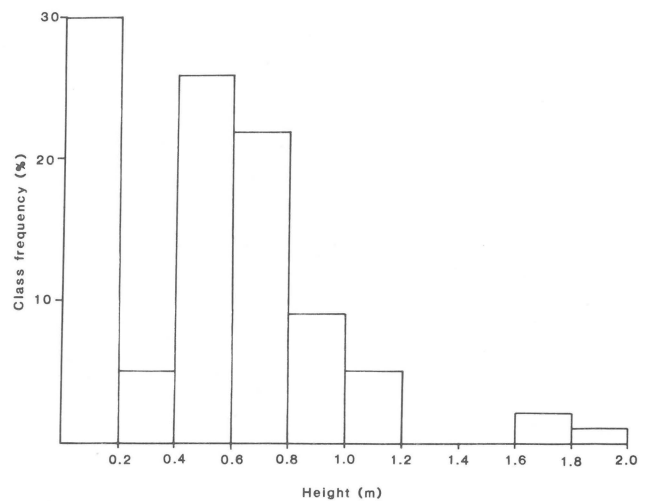


Figure 1 Height-frequency histogram for an *Aloe ferox* population at Fort Frederick ( $n = 93$ ).

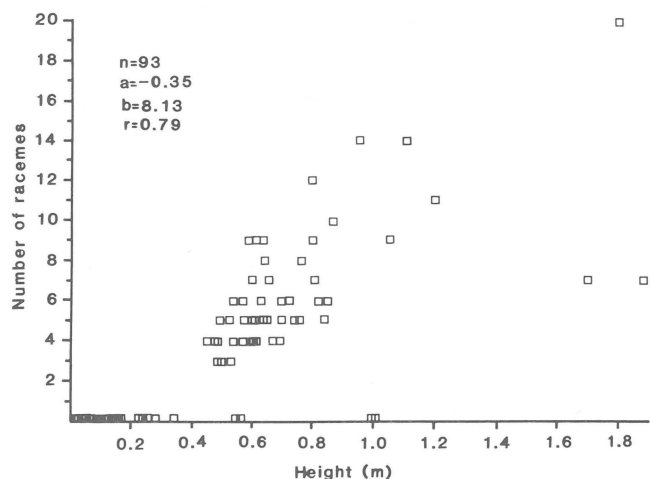


Figure 2 Plant height (m) versus raceme number for 93 plants at Fort Frederick.

was 0,5 m tall while two 1-m tall individuals failed to flower (Figure 2). The number of racemes per plant increased linearly with plant height (Figure 2). Three plants produced two inflorescences. The average number of racemes per plant was  $6,45 \pm 3,18$ . Raceme length (cm) ranged from 7,6 to 43,0 ( $x = 21,3 \pm 5,5$ ;  $n = 355$ ).

The number of flowers increased linearly with increasing raceme length ( $r = 0,93$ ,  $n = 20$ ,  $P < 0,005$ ) (Figure 3).

The average number of ovules per locule is  $64 \pm 4,0$  ( $n = 11$ ). There are thus about 192 ovules per flower. The number of seeds per capsule range from 40 to 86 ( $x = 65,7 \pm 13,6$ ;  $n = 33$ ). Therefore, in a single fruit about 66% of the ovules are either not fertilized or are aborted.

The correlation matrix (Table 1) shows that for the Fort Frederick population:

- The number of racemes increases linearly with plant height;
- Total raceme length is strongly correlated with the number of racemes and plant height but mean raceme length does not increase with plant height;
- The total number of fruits per plant increases as the plant becomes taller, as the number of racemes increases and as the total as well as the mean raceme length increase;
- Relative to the potential fruit production, there is no increase in percentage fruit success with increase in plant height, number of racemes and mean and total raceme length per plant.

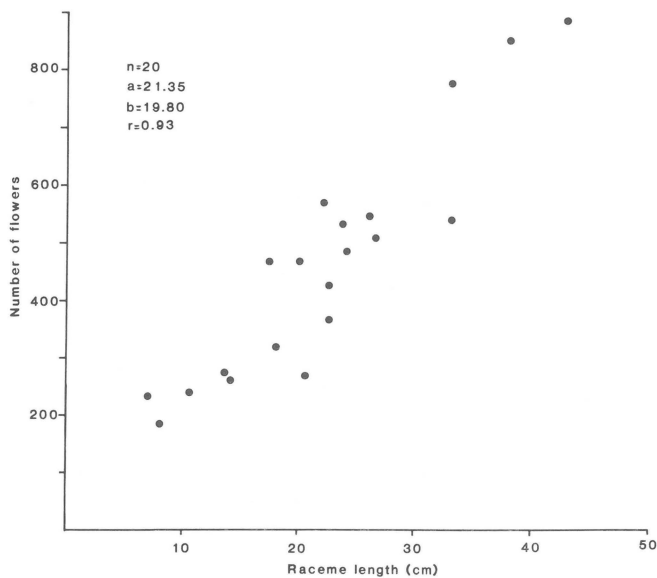


Figure 3 Number of flowers versus raceme length for 20 racemes from separate *Aloe ferox* plants in the Fort Frederick population.

### Floral morphology and development

The orange to yellow, ventricose buds open at any time of the day or night. The bisexual flowers mature acropetally and those on the north side (sunny side) of the raceme open first. The adaxial stamen is the first to emerge beyond the floral tube (Table 2, Figure 4). The style emerges together with the stamens and is loosely surrounded by the anthers for the first 24 h (Figure 4). At this point the small, white, capitate stigma has not yet expanded. After 32 h the style, filaments and perianth parts begin turning brown and some filaments become recurved. After 2 days all the filaments are recurved and the floral tube becomes shrivelled on day 3. Unfertilized flowers abscise approximately 4 days after anthesis.

The stigmas are receptive as soon as they emerge from the floral tube (Figure 5). The period of optimal stigma receptivity is between 8 and 24 h after anthesis and is synchronous with maximum nectar production. It appears that the period of optimal stigma receptivity does not correspond either with periods when the stigmatic surface is maximally expanded (on day 2) or with periods when an opaque sticky exudate appears on the stigmatic surface (on day 3). The stigma remains at least partially receptive for up to 4 days after anthesis (Figure 5).

For flowers opening in the morning, most of the anthers have been opened by honey bees within 4 h of anthesis. These insects, however, do not remove all the pollen and probably enough remains in the anthers to be carried by birds to other *A. ferox* plants. Many flowers on the raceme open during the night when bees are inactive. Such flowers, therefore still have anther sacs full of pollen 12–15 h after

Table 2 Floral development in one *Aloe ferox* plant from a population at Fort Frederick 1 to 72 h after anthesis ( $\pm$  standard deviation)

Hours after anthesis	Length of stamen exerted <sup>1</sup> (mm)	Length of style exerted (mm)	Number of anthers visible	Number of anthers open <sup>2</sup>	n
1	1,9 $\pm$ 1,1	not visible	1,4 $\pm$ 0,8	0	14
2	3,9 $\pm$ 1,2	0,6 $\pm$ 0,8	2,9 $\pm$ 1,4	0,4 $\pm$ 0,5	15
4	9,6 $\pm$ 2,1	4,3 $\pm$ 1,4	5,1 $\pm$ 0,5	4,3 $\pm$ 0,7	15
6	13,3 $\pm$ 0,9	8,0 $\pm$ 1,6	5,9 $\pm$ 0,3	5,7 $\pm$ 0,8	10
8	14,0	10,0	6	6	1
24	19,0 $\pm$ 0,4	15,3 $\pm$ 1,2	6	6	5
48	17,9 $\pm$ 1,1	17,3 $\pm$ 0,6	6	6	10
72	shrivelled	16,5 $\pm$ 1,2	–	–	4

<sup>1</sup>All measurements were taken from the end of the abaxial (longest) outer perianth part to the longest stamen or to the end of the stigma

<sup>2</sup>Pollinators were not excluded and bees were observed opening the anther sacs

Table 1 Spearman rank correlation coefficients for correlations between plant height, raceme length, fruit set and percentage success for an *Aloe ferox* population<sup>1</sup> at Fort Frederick, Port Elizabeth

	Plant height	No. of racemes	Total raceme length	Mean raceme length	Total no. of fruits/plant	Mean no. of fruits/raceme
No. of racemes	0,79***					
Total raceme length	0,45***	0,85 ***				
Mean raceme length	-0,16 <sup>ns</sup>	0,01 <sup>ns</sup>	0,54 ***			
Total no. of fruits/plant	0,43***	0,72 ***	0,75 ***	0,34**		
Mean no. of fruits/raceme	0,02 <sup>ns</sup>	0,24 *	0,27 **	0,19 <sup>ns</sup>	0,41***	
% success	0,01 <sup>ns</sup>	0,004 <sup>ns</sup>	0,004 <sup>ns</sup>	0,01 <sup>ns</sup>	0,55**	0,34**

<sup>1</sup> $n = 93$  for plant height vs. no. of racemes and  $n = 55$  for all other measurements

\* $P < 0,05$ ; \*\* $P < 0,01$ ; \*\*\* $P < 0,001$ ; <sup>ns</sup> not significant

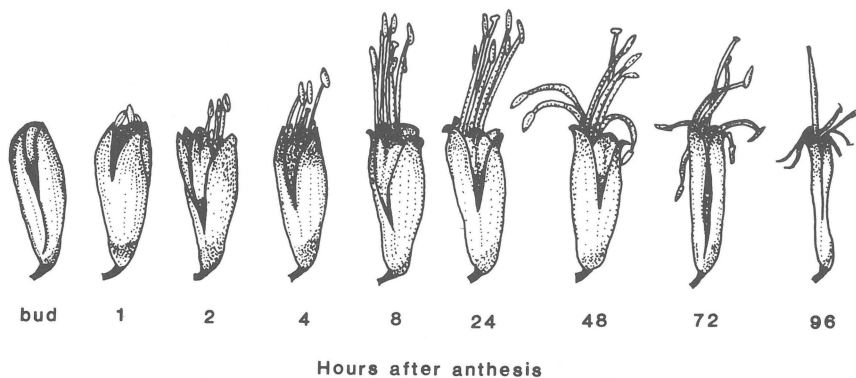


Figure 4 Stages of flower growth in *Aloe ferox*. The flowers are from one plant from the Fort Frederick population.

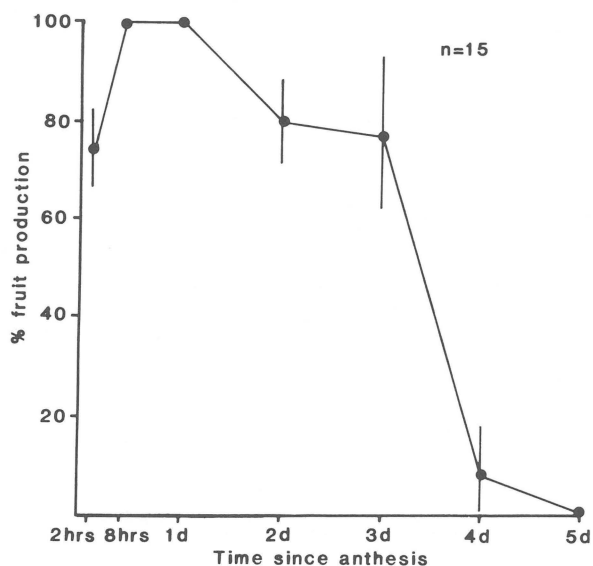


Figure 5 Flower age and fruit set in 15 *Aloe ferox* flowers from the University of Port Elizabeth gardens.

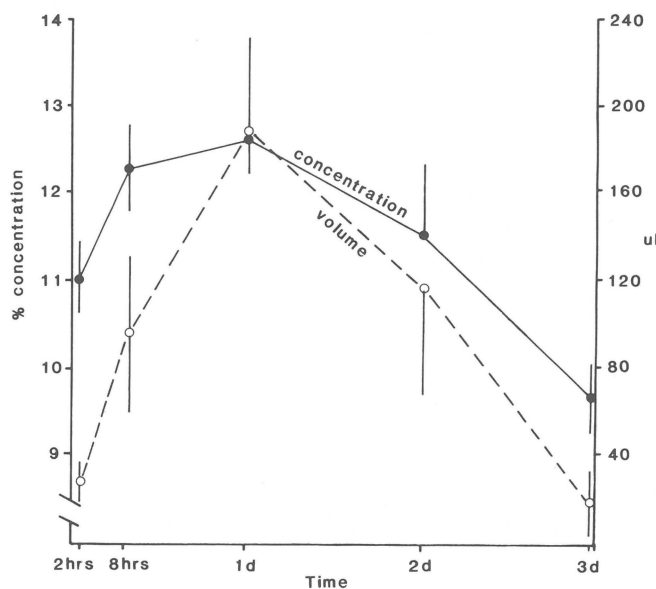


Figure 6 Nectar volume ( $\mu$ l) and concentration [(g sucrose equivalents per 100 g solution) %] versus time in 10 flowers from one *Aloe ferox* plant growing in the University of Port Elizabeth gardens.

anthesis and are only then visited for the first time by pollinators, whether they be birds or insects.

**Nectar**

Measurable nectar secretion begins after anthesis and continues for up to 3 days (Figure 6). Nectar volume and concentration peaks at 24 h after anthesis, and maximum production is asynchronous with regard to pollen presentation.

**Floral visitors**

A variety of insects and birds visited the racemes (Table 3). However, probably not all visitors transfer pollen to stigmas. Although I did not make detailed notes on bird pollinator behaviour, all bird visitors, with the exception of the streakyheaded canary, alight either on the raceme itself by grasping the flowers or perch on an inflorescence branch. From one of these positions they probe individual flowers for nectar, and in so doing cover their head, throat and breast with pollen, before moving to other racemes or plants. The streakyheaded canary is a destructive forager, usually standing on top of the raceme while removing flowers in search of nectar.

The formicine ant species was a rare visitor and probably plays little or no role in the pollination of this species. The chalcid wasps and unidentified dipteran species are too

**Table 3** Birds and insects visiting *Aloe ferox* at Fort Frederick during July 1986

Species	Behaviour <sup>1</sup>	Frequency <sup>2</sup>
<b>Aves:</b>		
<i>Onychognathus morio</i> (redwinged starling)	P	r
<i>Nectarinia amethystina</i> (black sunbird)	P	r
<i>N. chalybea</i> (lesser doublecollared sunbird)	P	r
<i>Ploceus capensis</i> (Cape weaver)	P	o
<i>Serinus gularis</i> (streakyheaded canary)	D	o
<b>Insecta:</b>		
<b>Hymenoptera:</b>		
<i>Apis mellifera</i> (African honey bee)	P	v
<i>Allodapula variegata</i> (allodapine bee)	P	c
<i>Lasioglossum</i> sp. A (sweat bee)	P	o
<i>Lasioglossum</i> sp. B (sweat bee)	P	o
<i>Camponotus</i> sp. (formicine ant)	V	r
Chalcidoidea (chalcid wasp)	V	c
<b>Diptera:</b>		
Syrphidae (hover fly)	P	r
Unidentified	V	c

<sup>1</sup>Behaviour: D=destructive forager, P=pollinator, V=visitor (see text for explanation)

<sup>2</sup>Frequency: r=rare (1 visit), o=occasional (2-10 visits), c=common (10-100 visits), v=very common (>100 visits)

**Table 4** The number of *Apis mellifera* visits per hour ( $\pm$  standard deviation) on one day for five flowers on one *Aloe ferox* raceme at Fort Frederick

Time	Hours after anthesis	No. of visits per hour
10h00	0	0
11h00	1	0
12h00	2	14,0 $\pm$ 6,0
13h00	3	14,4 $\pm$ 6,2
14h00	4	1,6 $\pm$ 0,9
15h00	5	0,8 $\pm$ 1,1
16h00	6	0

small (< 3 mm) to be effective pollinators and were never observed on the anthers or stigma.

The most frequent visitor was the honey bee. Individuals would usually alight on opened flowers and those of 2 to 3 h post-anthesis age were preferred (Table 4).

Bees landed on and opened the adaxial anther first. The other anthers were visited as they emerged beyond the floral tube. Visitation time ranged from 2 to 45 secs ( $x = 12 \pm 13$  secs;  $n = 22$ ). The longest visits were to newly exerted anthers. Flowers were sometimes visited alternately but no directional movement (i.e. up or down the raceme) was apparent. Bees normally visited only a few flowers from one or two inflorescences before leaving the population. The data in Table 4 were collected on a single sunny, windless day and are from a small sample. While general field observations corroborate these findings there appears to be great variation in visitation times. The presence of bees appears to be partly dependent on weather conditions. In this study, rain or strong winds precluded their visits.

On a few occasions I saw bees taking nectar from flowers. To do this they moved between the flowers and inserted their proboscis as close to the base of the flower as possible, positioning themselves far from the anthers. They thus appear to be ineffective pollinators when taking nectar. I did not observe these insects climbing into the flower in search of nectar as Skead (1967) suggests, although this is possible and may occur.

#### Breeding system

*Aloe ferox* is self-incompatible within the limits set by Bawa (1974) (i.e. not more than 33% of the self-fertilized flowers should produce fruit and/or cross-pollinations should produce five times the number of fruit than self-pollinations) (Table 5).

**Table 5** Comparison of fruit set in *Aloe ferox* for cross, geitonogamous, control (bagged but not manipulated) and open pollinations ( $\pm$  standard deviations) <sup>1</sup>range = 0,2–56,4

Treatment	No. of plants	No. of flowers	% success
Cross	2	212	80,0 $\pm$ 10,5
Geitonogamous	2	244	5,9 $\pm$ 3,7
Control	4	1569	0,3 $\pm$ 0,5
Open	55	24420	26,8 $\pm$ 13,3 <sup>1</sup>

#### Discussion

For *A. ferox*, plant age is correlated with height (Holland & Fuggle 1982). The height–frequency histogram for the Fort

Frederick population suggests intermittent, successful recruitment years followed by poor or no recruitment.

For some species, percentage fruit success (the number of fruits produced as a percentage of the number of flowers available) increases with the number of flowers per inflorescence (Willson & Rathcke 1974; Willson & Price 1977; Schaffer & Schaffer 1977; Stephenson 1980), and plant height (Pyke 1981). It is suggested that pollinators are preferentially attracted to larger and more conspicuous inflorescences (Pyke 1981). This agrees with optimal diet selection theory in which pollinators, attempting to maximize their rate of caloric intake, concentrate preferentially on larger inflorescences with greater rewards (Schaffer & Schaffer 1977). It follows that for the plant, reproductive success, in terms of efficiency on a per-flower basis, would be greater for larger and more conspicuous inflorescences. These relationships did not hold for the Fort Frederick *A. ferox* population but its location within an urban environment may have influenced this considerably. Measurements from undisturbed, 'wild' populations may provide different results.

For this self-incompatible species the advantages of producing an inflorescence with a greater number of racemes or a raceme with more flowers are unclear. While greater rewards may be offered to pollinators, only a small number of flowers on any raceme will be cross-pollinated before the pollinator becomes saturated with pollen from the same raceme. The selection pressure has probably rather been to limit the number of open flowers on a raceme at any one time. While the orange buds may still serve to attract pollinators to an inflorescence, such pollinators will find suitable rewards in a few flowers only and will therefore be forced to move to another inflorescence on a different plant. This minimizes the chance of self-pollination and increases the transference of pollen to conspecifics (male fitness). It is not surprising that *Aloe broomii*, which often occurs as widely separate individuals, should produce a single raceme with very few flowers open at any one time (Skead 1967). Cross-pollination is thereby maximized.

Most species within the tribe Aloineae are self-incompatible (Brandham 1969; Riley & Majumdar 1979). The number of fruits derived from self-pollinations in this study were relatively high compared to other studies on the group. Brewbaker & Gorrez (1967) for example, obtained no capsules from over 3 000 self-pollinations in two *Gasteria* species. In their experiment, the self-incompatibility reaction appeared not to be at the stigmatic surface but lay rather in the development of the integuments of the ovule. In *Gasteria* an incompatible pollen tube apparently inhibits ovule integument development (Riley & Majumdar 1979).

The floral and inflorescence morphology of *Aloe ferox* strongly suggests a bird-pollinated syndrome but the incidence and the possible involvement of insects in pollination should not be ignored (Skead 1967; Baker 1983). This study suggests that, for *A. ferox*, both insects and birds may be important pollinators. The plant offers different rewards to different pollinators. For honey bees, pollen appears to be the chief reward and as soon as the anthers emerge they are opened and most of the pollen removed. The stigma is at least partially receptive at this stage and because it is surrounded by the anthers, pollen transfer by insects is easily effected. Although it was not tested, it seems reasonable to assume that insects carry pollen over shorter distances than birds. The chance that pollen comes from another *A. ferox* individual and not from a flower within its own raceme or inflorescence, is therefore, probably greater when carried by a bird than by an insect. Nectar is the chief reward offered to bird pollinators and nectar volume and concentration and optimal stigma receptivity schedules are

synchronized. By having a stigma which is at least partially receptive throughout the period during which rewards are offered to pollinators, *A. ferox* capitalizes on two divergent pollinator groups. Optimal receptivity, however is synchronous with periods when maximum outcrossing is most likely.

In conclusion, this study confirms earlier worker's (Skead 1967; Baker 1983) predictions that *Aloe* does exploit divergent pollinator groups and that in *Aloe ferox*, an outcrossing species, this relationship has centered on birds and bees. This study may also serve as a warning to those who automatically assign plants to a particular category of pollinator class on the basis of flower colour and structure.

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