

## PARTITIONING OF POLLINATORS DURING FLOWERING IN AN AFRICAN ACACIA COMMUNITY

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**Abstract.** Competition for pollination is an important factor structuring flowering in many plant communities. We examined mechanisms reducing interspecific pollen flow in a community of 10 *Acacia* species in a highly seasonal savannah habitat in Tanzania. Partitioning is achieved, in part, through separation of flowering in space and seasonal time, and through interspecific differences in pollinator guilds. Nevertheless, coflowering *Acacia* species shared several pollinators; this means that interspecific pollen transfer is possible. We analyzed daily patterns of pollinator activity and pollen release in 10 *Acacia* assemblages containing a total of 10 *Acacia* species. Pollinator activity was scored using counts at flowers over constant time intervals throughout the day. Pollen availability was assessed using a simple method which allows quantification of pollen exposed on the surface of the *Acacia* inflorescence. Sympatric co-flowering *Acacia* species each show high intraspecific synchrony but release their pollen at different times of day. Pollinators rapidly harvest available pollen and move from one *Acacia* species to the next, following the daily sequence of pollen release. The activity of shared pollinators is structured throughout the day as a result of temporal patterns of pollen release across *Acacia* species. The observed temporal structuring of pollen release is compatible with patterns predicted to result from competitive displacement. Additional support for a competition-based explanation for this patterning comes from the observation that an *Acacia* species flowering without competitors shows no synchronized peak of pollen availability at any time of day.

**Key words:** *Acacia*; bees; character displacement; competition; dehiscence; niche; pollination; resource partitioning; Tanzania.

### INTRODUCTION

Flowering plants may compete for pollination in at least two ways; for pollen quantity, and for pollen quality (Rathcke 1983, 1988). In cases where the quantity of pollen exchanged is a limiting factor for seed set, plants may compete for pollinator visits (Mosquin 1971, Bierzychudek 1981, Horvitz and Schemske 1988). In other cases, the purity of the pollen pollinators carry, rather than the number of visits they make, is the controlling factor. If pollinators visit a mixture of flowering species over a short period, some proportion of the pollen they deposit on stigmas may be heterospecific. Heterospecific pollen transfer has the potential to reduce reproductive success in two ways: male-function may be reduced through deposition on heterospecific stigmas, while female function may be reduced through physical blocking of limited stigmatic surface with heterospecific pollen (Waser 1978*a, b*, 1983, Waser and Fugate 1986, Fishbein and Venable 1996). Evidence to date suggests that avoidance of heterospecific pollen transfer is more important than

competition for pollinator visits in natural systems (Waser 1983, Rathcke 1983, 1988) and minimization of the costs associated with either mechanism of competition is thought to be an important force structuring plant communities (Pleasants 1983, Rathcke 1983, 1988, Waser 1983, Armbruster and Herzig 1984, Rathcke and Lacey 1985, Feinsinger 1987).

An expected evolutionary consequence of competition is divergence along some resource axis (resource partitioning) to reduce the negative interaction between coexisting species (Brown and Wilson 1956, Pianka 1973, Schoener 1983). Four resource axes have received attention. First, plants may differ in the pollinators they recruit (axis 1), and so have independent vectors of pollen transfer (Heinrich 1976, Inouye 1978, Pleasants 1983, Armbruster and Herzig 1984, Rathcke 1988). However, pollinator guilds of plant species often overlap and many studies have examined mechanisms that partition the activity of shared flower visitors (Waser 1978*a, b*, Feinsinger 1983, Kephart 1983, Schemske 1983, Armbruster 1985, Campbell and Motten 1985, Waser and Fugate 1986, Rathcke 1988). Plants in the same pollinator guild may utilize effectively independent populations of the same pollinator species (and thus avoid competition) through separation in space (axis 2) (Pleasants 1980, Rathcke 1988) or in seasonal

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time (axis 3) (Levin and Anderson 1970, Mosquin 1971, Heithaus 1974, Poole and Rathcke 1979, Pleasants 1980, 1983, Kephart 1983, Rathcke 1983, Ashton et al. 1988). Relatively few studies have directly examined the effects of such putative mechanisms on the activity of shared pollinators (Waser 1978*a, b*, Pleasants 1980, Waser 1983, Campbell 1985, Armbruster and McGuire 1991, McGuire and Armbruster 1991, McGuire 1993).

An increasing number of studies, however, show that sympatric species may share pollinators and have overlapping flowering seasons. Such clustering may result through limited divergence of contemporary species from ancestral patterns of flowering (Kochmer and Handel 1986, Wright and Calderon 1995) or from constraints on flowering imposed by seasonal patterns in the availability of resources such as water or thermo-period (Janzen 1967, Hocking 1968, Reich and Borchert 1984, Rathcke 1984, 1988, Johnson 1992). A fourth resource axis allowing such co-flowering species to share pollinator individuals is the utilization of discretely different parts of the pollinator's body for pollen transport (axis 4) (Dressler 1968, Armbruster et al. 1994). A further possibility is the evolution of floral traits, such as increased floral longevity, that confer tolerance of competition (Levin 1978, Motten 1986, Rathcke 1988, Ashman and Schoen 1994).

An alternative is for plant species to diverge along an additional resource axis: daily time (axis 5). Divergence among co-flowering species in their timing of pollen release (dehiscence) through the day could reduce competition in two ways (Levin and Anderson 1970, Ollerton and Lack 1992). First, daily partitioning of resource availability could result in temporal partitioning of pollinator behavior, so that co-flowering plants avoid competition for pollinator visits. Second, because many pollinators remove pollen from their bodies at regular intervals (Gilbert 1981, Roubik 1989), temporal partitioning of their activity will result in pollinators carrying predominantly one type of pollen at any one time, so reducing interspecific pollen transfer. Both mechanisms allow sympatric co-flowering plants to share both flowering seasons and pollinators.

Few studies have examined in detail the daily activity patterns of shared pollinators at the flowers of potentially competing plants (but see Armbruster and Herzig 1984, Armbruster 1985, Stone et al. 1996), despite the fact that these patterns may have important consequences for the inference of competition in plants whose flowering seasons overlap. Two plants with identical flowering seasons and pollinators may indeed compete if pollinators visit them indiscriminately during the day, but competition may be substantially reduced if the pollinators' daily activity patterns at the two plants are entirely separated. The importance of daily structuring in competition for pollination is unclear. Although shared pollinators are known to visit particular plant species at different times of day (Frankie

et al. 1983, Stone 1994), most analyses of flowering phenology have addressed seasonal phenology and lack the necessary resolution to examine daily patterns.

Tanzanian *Acacia* trees (Leguminosae; Mimosoideae; genus *Acacia*) provide a clear example of daily patterning, both of pollen release and pollinator activity (Stone et al. 1996). While members of each of four *Acacia* species showed highly synchronized anther dehiscence, daily peaks of pollen release were regularly spaced across species, as predicted for generation of the observed patterning by competitive character displacement (Pleasants 1980, Waser 1983, Williams 1995). Such patterning could also result from ecological sorting (through differential colonization and/or extinction rates) of species that differ in their timing of pollen release for other reasons (Armbruster 1985, 1986). The long evolutionary history of East African savannahs and the geographically stable structure of *Acacia* communities (Ross 1981, Kingdon 1990) both suggest that long-term evolutionary responses, rather than ecological sorting, are responsible for the patterns seen in Tanzania. Three factors may predispose *Acacia* species to the exploitation of the daily time resource axis. First, they commonly grow in mixed-species assemblages and several species flower together in space and time after seasonal rainfall (Ross 1981). Second, the scented and showy inflorescences of *Acacia* species are visited by a wide diversity of flower visitors, at least some of which are shared by more than one *Acacia* species (Bernhardt 1987, Tybirk 1989, 1993, Stone et al. 1996). Third, the structure of *Acacia* flowers is very similar across sympatric species, and there is no a priori reason why pollen collected from one species cannot be deposited on flowers of another. Segregated pollen flow among species through deposition of pollen on different regions of shared pollinators, known for a few other plant pollination guilds (Dressler 1968, Armbruster et al. 1994), is thus unavailable to *Acacia*.

In this study, we present a more detailed analysis of flowering in the same Tanzanian *Acacia* community discussed in Stone et al. (1996), and ask the following questions:

- 1) What are the intra- and interspecific patterns of pollen release in seasonal and daily time, and are these patterns consistent among sites and among years?
- 2) Do correlations between microclimatic variables and the timing of pollen release provide any indication of which cues could structure differences among species, if present?
- 3) Do interspecific differences in the timing of daily pollen release provide evidence of character displacement among co-flowering *Acacia* species?
- 4) Does the provision of different floral rewards (pollen vs. nectar) by *Acacia* species generate differences in the assemblages of flower visitors they attract? Do co-flowering *Acacia* species share flower visitors likely to be significant pollen vectors, and hence pos-

sible agents of selection for divergence in the timing of daily pollen release?

5) Do differences in timing of pollen release among co-flowering *Acacia* species generate corresponding structure in the activity of shared pollinators?

Flowering is highly variable in space and time (Keshphart 1983, Ashman and Stanton 1991), and an understanding of intraspecific variation is essential if the evolutionary significance of patterns across species is to be assessed (Spieth 1979, Connell and Sousa 1983, Motten 1986, Horvitz and Schemske 1990, Neff and Simpson 1990, Minckley et al. 1994). We thus examine intraspecific variation in the daily timing of pollen release among individuals, among days, among sites, and between years, and then extend our analysis to patterns across species.

An explanation for the regular spacing of daily pollen release across species based on character displacement (Stone et al. 1996) leads to two predictions that we test in this study. The first prediction is that species that flower alone in seasonal time should not have been exposed to selection for intraspecific synchrony in pollen release. Subject to any other constraints in operation, these species are expected to release pollen over a broader time period through the day.

The second prediction is that the daily time niche occupied by an *Acacia* species might be sensitive to spatial variation in local competition. Thus, if populations of a species have a long history of exposure to differing sets of competitors, we might expect to see ecotypic differentiation among those populations in timing of pollen release (Armbruster 1985). We test whether there is any evidence of such intraspecific variation, and whether such variation, if found, can be associated with particular *Acacia* species interactions.

Demonstration of resource partitioning in daily time has two components: (a) patterning of pollen release in the component *Acacia* species and (b) a corresponding patterning in the activity of the shared pollinators that are the presumptive agents of interspecific pollen transfer, and hence of selection (Pleasants 1980, 1983, Rathcke 1988, Neff and Simpson 1990, Minckley et al. 1994). Here we match daily activity patterns of shared pollinators with variation in pollen availability in *Acacia* species in order to assess the functional consequence of apparent resource partitioning.

## METHODS

### *Study sites and study species*

This study was carried out between November 1994 and January 1997 in the Mkomazi Game Reserve in northern Tanzania (Fig. 1). The study area consists of *Acacia-Commiphora* bush at an altitude of 700–1000 m with a highly seasonal pattern of rainfall (Harris 1972, Coe and Beentje 1991). The main (autumn) rains fall between November and January, with a second and more diffuse period of rainfall from April to early June.

Ten *Acacia* species, representing the two *Acacia* subgenera present in Africa (Ross 1981), were studied in an area 20 × 50 km at the western end of the reserve (Fig. 1). *Acacia brevispica* Harms, *A. drepanolobium* Sjöstedt, *A. etbaica* Schweinf., *A. nilotica* (L.), *A. reficiens* Wawra, *A. tortilis* (Forssk.) Hayne, and *A. zanzibarica* (S. Moore) are members of the subgenus *Acacia*, while *A. bussei* Sjöstedt, *A. senegal* (L.) Willd., and *A. thomasii* Harms are members of the subgenus *Aculeiferum* (Ross 1981).

In Mkomazi, characteristic *Acacia* assemblages are associated with particular soil types (Harris 1972). We selected 10 sites (Fig. 1) with different *Acacia* assemblages, listed in Table 1. Six sites were located on poorly drained valley bottom soils (Kisima Road, Kisiwani Road, Ngurunga Road and Pat's Rock; Fig. 1), which support *Acacia bussei*, *A. etbaica*, *A. reficiens*, *A. senegal*, and *A. zanzibarica*. Where the site also contained seasonally saturated black cotton soils (Pangaro and Ubani; Fig. 1), this assemblage was joined by *A. drepanolobium*. Three sites were located on well-drained valley soils and the lower slopes of hills (Hunters' Camp, Zange Gate, Vitiwini Road; Fig. 1), which typically harbor *A. nilotica*, *A. senegal*, and *A. tortilis*. We sampled one site located on a rocky hill slope (Simba Hill; Fig. 1), where the latter species were present in low numbers, joined by *A. brevispica* and *A. thomasii*. *Acacia thomasii* is a specialist of rocky slopes, and is often the only *Acacia* abundant in such habitats in Mkomazi (Harris 1972). Ubani and Pangaro sites contained mosaics of different soil types and supported the greatest richness of *Acacia* species. Species listed as present at a site in Table 1 were found within 100 m of each other. In order to investigate possible intraspecific differences between sites, we selected sites as widely separated as logistically possible (10–30 km; Fig. 1).

### *Determining patterns of pollen and nectar availability through time*

Flowers of *Acacia* species in the subgenus *Aculeiferum* are usually borne on elongated inflorescences and produce nectar, while those of species in the subgenus *Acacia* are usually presented in spherical inflorescences and without nectar (Plate 1). The flowers of both subgenera are typically protandrous, and last for a single day (Tybirk 1989, 1993, Stone et al. 1996, Willmer and Stone 1997). Individual inflorescences last for a single day for the study species in the subgenus *Acacia*, while species in the subgenus *Aculeiferum* have inflorescences in which discrete sets of flowers along the inflorescence axis open over 2–3 d. Individual *Acacia* flowers consist of a narrow corolla tube occupied by many stamens (Tybirk 1993). Presence or absence of nectar was determined by inserting a 1 µL micropipette (Camlab, UK) drawn out to a fine point into individual flowers. Nectar volume was determined from the length of the nectar column in the micropi-

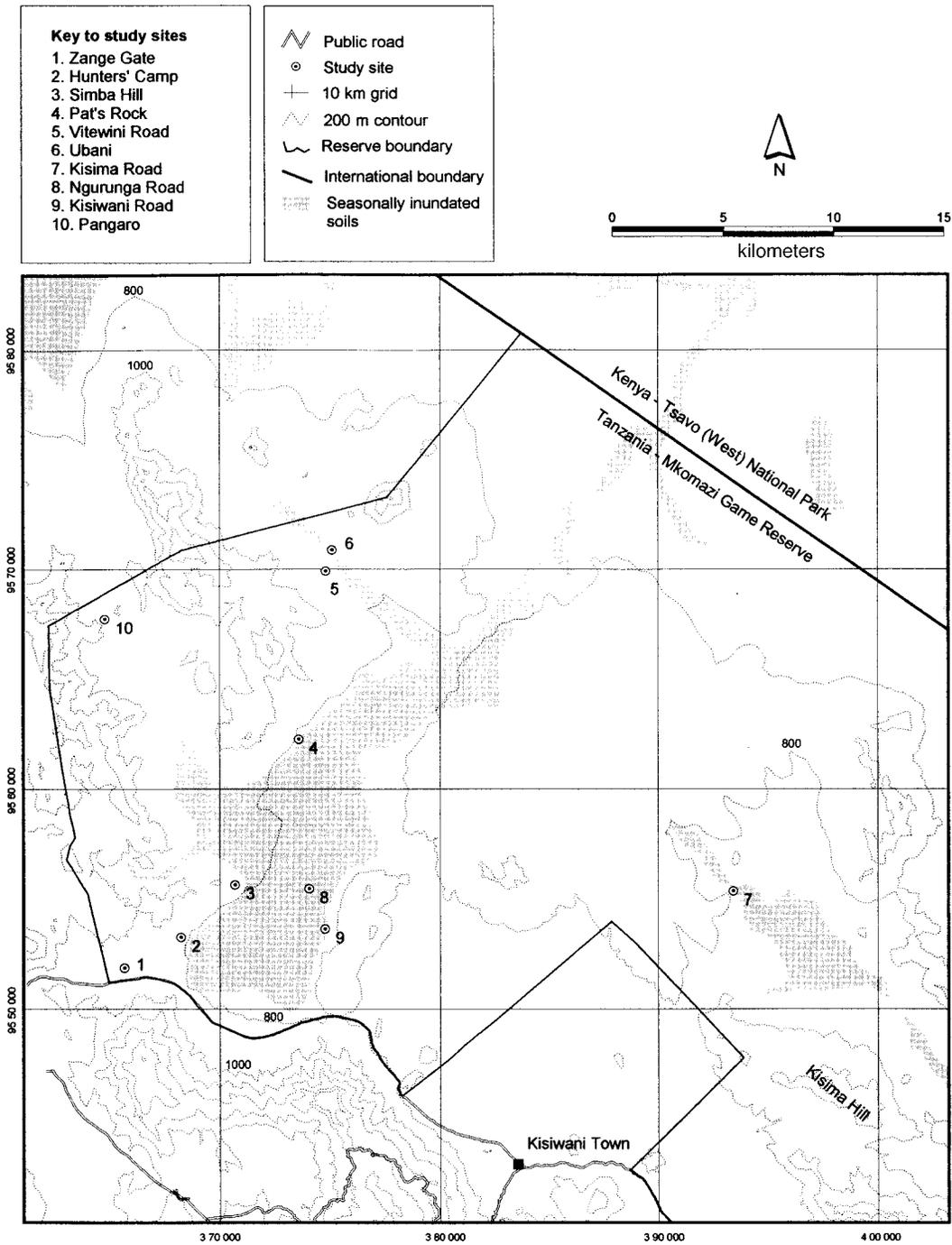


FIG. 1. A map of the study area. The superposed grid is of 10 × 10 km squares, and the shaded areas represent seasonally inundated soils.

pette, and sucrose concentration was measured using a hand-held refractometer specially modified for very low volumes (Bellingham and Stanley, UK).

*Acacia* pollen is presented in the form of compound polyads (Knox and Kenrick 1982), with eight polyads per anther. Pollen release (dehiscence) in each species was evaluated by examining the relative abundance of

pollen available on the surface of inflorescences sampled at intervals through the day. For each *Acacia* species, at each sample time, two to three inflorescences were chosen randomly with respect to aspect and height above ground and removed from the tree without touching the inflorescence surface. Each sampled inflorescence was rolled lightly across the adhesive side of a

TABLE 1. *Acacia* species composition at the chosen study sites (p = present).

<i>Acacia</i> species	Site									
	Zange Gate	Hunters' Camp	Simba Hill	Pat's Rock	Vitiwini Road	Ubani	Kisima Road	Ngurunga Road	Kisiwani Road	Pangaro
<i>A. brevispica</i>			P							
<i>A. bussei</i>					p	p	p	p		p
<i>A. drepanolobium</i>										p
<i>A. etbaica</i>					p	p				p
<i>A. nilotica</i>			P			p				p
<i>A. reficiens</i>				P	p	p	p	p		p
<i>A. senegal</i>	p	p	p		p	p	p			p
<i>A. thomasii</i>			p							
<i>A. tortilis</i>	p	p	p							p
<i>A. zanzibarica</i>				p	p	p	p	p	p	

piece of clear adhesive tape. The tape was then placed sticky-side down over a microscope slide and examined with a light microscope. The progress of dehiscence over time was recorded by scoring the ratio of anthers to polyads collected on the tape. Prior to dehiscence, only unopened anthers were collected. Once anthers began to dehiscence, polyads were also collected: the numbers increased as dehiscence took place, and then decreased as they were removed by pollinators. For each

inflorescence, the ratio of anthers to polyads was recorded for three to five randomly chosen microscope fields and the mean calculated. For each *Acacia* and time interval, the mean ratio was calculated across the sampled inflorescences. Standardizing the range in pollen to anther ratios among trees is necessary in order for each tree to contribute equally to means calculated across trees, days, or sites. Pollen to anther ratios were therefore constrained to vary between zero and one for

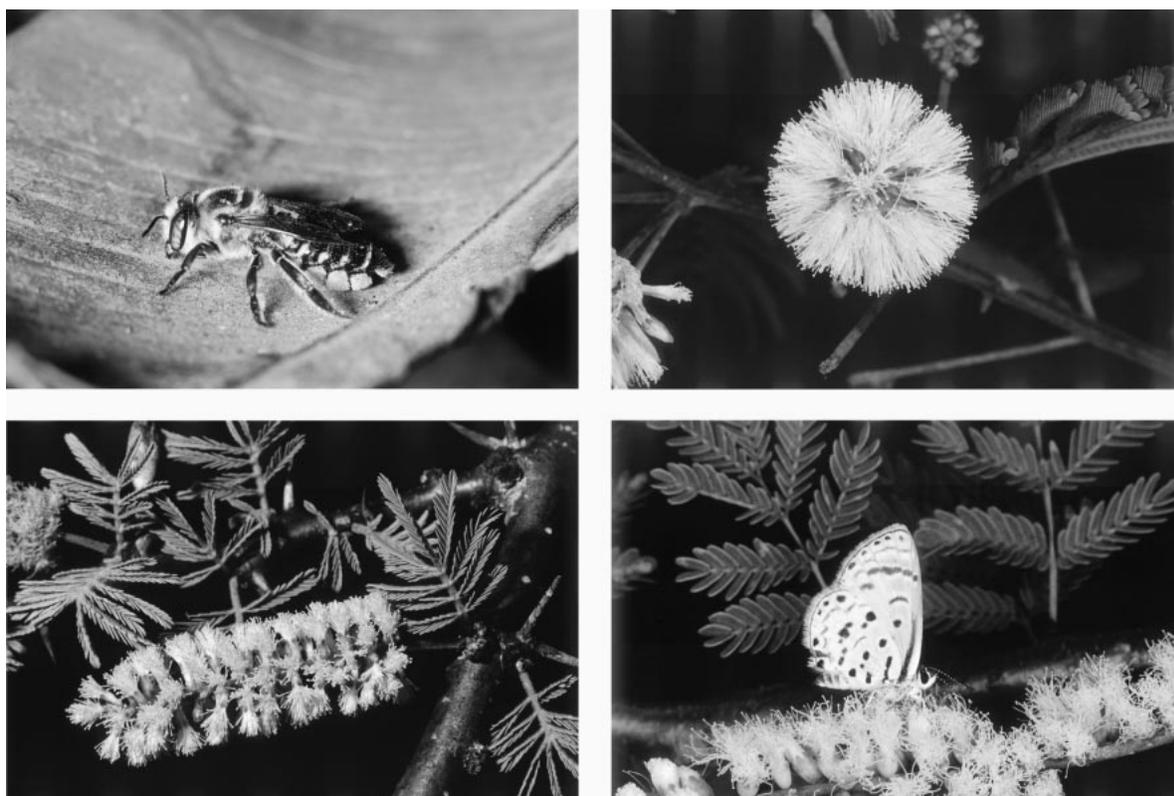


PLATE 1. (Top left) The small megachilid bee shared as a pollinator by Mkomazi acacias, showing pollen stored in a ventral scopa on the underside of the abdomen. (Top right) The spherical (globose) inflorescence of *Acacia brevispica* (this inflorescence structure is characteristic of species in the *Acacia* subgenus *Acacia*). (Bottom left) The elongate (spicate) inflorescence of *Acacia bussei* (this inflorescence structure is characteristic of species in the *Acacia* subgenus *Aculeiferum*). (Bottom right) A lycaenid butterfly (*Azanus ubaldus*) feeding on nectar from flowers of *Acacia senegal*.

TABLE 2. Summary of the sampling effort (for both pollen release and flower visitation) associated with each *Acacia* species at each site.

<i>Acacia</i> species	Site	Pollen sampling effort (in tree days)	Visitation (trees watched)	Date
<i>A. brevispica</i>	Kisima Hill	1	0	3 Jan 1997
	Simba Hill	1	1	4 Sep 1996
	Simba Hill	part days	0	6–10 Jan 1996
<i>A. bussei</i>	Ngarunga	2	2	22 Dec 1996
	Ngarunga	2	2	23 Dec 1996
<i>A. drepanolobium</i>	Ubani	2	2	9 Dec 1995
	Ubani	4	4	12 Jan 1997
<i>A. nilotica</i>	Pangaro	2	0	13 Jun 1996
	Ubani	0	2	8 Dec 1995
	Ubani	2	2	9 Dec 1995
	Ubani	0	1	19 Dec 1995
	Ubani	3	3	12 Jan 1997
	Pangaro	2	0	13 Jun 1996
<i>A. senegal</i>	Kisima Road	3	3	4 Jan 1997
	Ubani	1	1	19 Dec 1995
	Ubani	8	2	13 Jan 1997
	Vitiwini Road	2	2	29 Dec 1996
	Zange Gate	1	1	9 Jan 1997
	Zange Gate	1	1	10 Jan 1997
<i>A. thomasii</i>	Simba Hill	2	0	29 Jul 1996
	Simba Hill	2	0	4 Aug 1996
<i>A. tortilis</i>	Hunter's Camp	2	0	8 Jan 1997
	Zange Gate	4	4	9 Jan 1997
	Zange Gate	3	3	10 Jan 1997
<i>A. zanzibarica</i>	Kisima Road	3	0	4 Jan 1997
	Kisiwani Road	8	2	6 Jan 1997
	Ngurunga	2	0	22 Dec 1996
	Ngurunga	3	3	28 Dec 1996
	Pat's Rock	2	0	18 Nov 1995
	Pat's Rock	2	0	20 Nov 1995
	Pat's Rock	2	2	21 Nov 1995
	Pat's Rock	0	2	22 Nov 1995
	Pat's Rock	2	2	24 Nov 1995

each individual tree and day by dividing them by the maximum value recorded at any time interval for that tree and day. Differences among sites in patterns of pollen availability through time were analyzed with two-way ANOVA of the standardized pollen/anther ratios. All proportion data were arcsine transformed prior to analysis (Sokal and Rohlf 1981).

The sampling effort devoted to analysis of pollen release in each species is summarized in Table 2. Additional data on seasonal patterns of flowering were recorded during the autumn rains in 1994–1995. Data on intraspecific variation in timing of pollen release were obtained by concentrating sampling effort on *A. zanzibarica* and *A. senegal*, both of which grow widely in the study area in a range of *Acacia* species assemblages (Table 1). For these species we obtained data on variation among individuals at a given site on the same day, variation in the same individual between years, and variation among sites in the same flowering season. Data allowing comparison between years for the same individuals were also obtained for *A. nilotica*, *A. drepanolobium*, and *A. senegal*. Data allowing com-

parison between spring and autumn rains within the same year were obtained for *Acacia nilotica*.

Obtaining compatible data on pollen release in a range of species required certain unavoidable compromises in sample size. At each time interval, sampling effort had to be allocated between inflorescences on a given tree, trees of a given species, and other species at the same site. Time also had to be allocated to obtaining microclimate data and insect visitation data. The small numbers of tree days obtained for a given species shown in Table 2 at a given site on a given date reflect these compromises. Our allocation of sampling effort was based, in part, on the observation that earlier studies of the same *Acacia* populations showed little variation between individuals at a site in temporal patterns of pollen presentation (Stone et al. 1996).

#### *Recording of possible microclimatic cues triggering pollen release*

Timing of anther dehiscence in flowers is sensitive to a variety of environmental cues, particularly relative humidity (Percival 1965, Buchmann 1983, Corbet et

al. 1988). Differences between times of pollen release within a species between sites might therefore result from differences in microclimate rather than ecotypic differentiation. To allow separation of these effects we recorded temperature and relative humidity every hour during days on which pollen availability was scored. Data were obtained in the shade of the studied *Acacia* species at a height of 1 m with a Vaisala HMI 31 humidity and temperature probe. Use of a single measure of either of these variables to represent the microenvironment surrounding flowers is an oversimplification, and while more detailed data would clearly be desirable, obtaining them was precluded by the logistics of making other measurements. Because *Acacia* flowers are at different heights in different species (e.g., 1–2 m in *A. drepanolobium* and  $\leq 7$  m in *A. tortilis*), it is inappropriate to apply measurements obtained at a single set height to cross-species comparisons. We have therefore only used our microclimate data for intraspecific comparisons, where the relationship between measurement height and mean flower height is constant.

*Tests of structure in temporal patterns of pollen release across species*

Character displacement resulting from interspecific competition (or competitive displacement; Brown and Wilson 1956, Pleasants 1980, Williams 1995) reduces the overlap among species along a given resource axis, resulting in species values that are more regularly spaced than predicted by chance (e.g., Armbruster et al. 1994). Several methods have been developed to test temporal structure in flowering seasons (Poole and Rathcke 1979, Pleasants 1980, Cole 1981, Gleeson 1981, Fleming and Partridge 1984, Kochmer and Handel 1986), each comparing the observed spacing of flowering seasons to the null prediction that species' blooming periods are randomly distributed through time. The most appropriate statistic with which to test character displacement is the Var statistic, originally proposed by Poole and Rathcke (1979) (Pleasants 1994, Williams 1995). Use of Var in its original form is made complex by the need to perform a long series of randomizations in order to assess the statistical significance of values obtained. Williams (1995) provides a table of critical values of a statistic  $V$ , derived from Var, which greatly simplifies the detection of significant character displacement, and we use the  $V$  statistic here. For a given set of species values along a resource axis, calculation of  $V$  requires estimation of (1) the distances between successive species (first to second species, second to third species, etc.) and (2) the difference between the greatest and least values shown by the set of species in question, or range.  $V$  is then given by the expression:

$$V = \frac{\text{Sum of squares of the distances}}{(\text{number of species} - 1) \times (\text{range})^2}$$

The  $V$  statistic can be applied to any resource axis, and we use it to examine the spacing of daily peaks of pollen availability within and among *Acacia* species. Character displacement, if it has occurred, is predicted to result in two patterns in timing of pollen release: (1) intraspecific aggregation and (2) interspecific divergence. Both of these predictions can be tested using Williams'  $V$  statistic (Williams 1995).

*Intraspecific variation.*—If individuals of a species release their pollen at similar times, peaks of pollen availability for individuals will be aggregated in daily time. Testing for aggregation requires an assumption about the time period within which individuals may release their pollen, since the null hypothesis to be tested is that individual peaks of pollen availability are randomly distributed within this period. Because all of the flower visitors observed at *Acacia* trees were diurnally active species, and none of the *Acacia* species release its pollen at night, we assume the period available for visitor activity to be from sunrise to sunset (~0600–1800).

*Interspecific variation.*—Analysis of the spacing of flowering phenologies is often carried out between first and last species peaks (Pleasants 1980), which is appropriate where there are no a priori limits to the resource axis between which species values should be dispersed. Where limits can be identified, spacing is analyzed between limiting values along the resource axis. We apply both methods to interspecific patterns of pollen release, using dawn and dusk as biologically meaningful a priori limits to the resource axis, as justified above. The null hypothesis tested in each case is that the peaks of pollen availability are randomly distributed between the delimited values of time.

Analysis of patterning will also be sensitive to the species chosen. We have applied the  $V$  statistic to those *Acacia* species flowering after the autumn rains, when the species richness of co-flowering *Acacia* species is greatest. All of the species flowering at this time may potentially occur together due to variations in phenology between years or in soil-type mosaic structure, and we therefore include them all initially. We then describe the effect of removing from the assemblage three species that, though flowering over the same period, are least likely to overlap in space or time with the others: (1) *Acacia drepanolobium* is the only *Acacia* to grow on black cotton soils, and is rarely sympatric with the other *Acacia* species. (2) *Acacia tortilis* requires the best drained soils of the remaining species, and was never found in close proximity to species (such as *A. zanzibarica*) characteristic of wetter soils. (3) *Acacia bussei* is right at the end of its flowering season by the autumn rains, and is thus partially separated from the others in seasonal time.

*Temporal patterns of flower visitation and comparisons of visitor assemblages across Acacia species*

Detailed analyses of flower-visitor behavior were completed during the autumn rains in 1995–1996 and

TABLE 3. Seasonal flowering patterns of Mkomazi *Acacia* species. An "m" indicates mass flowering, and an "s" indicates slight, scattered flowering.

Season and <i>Acacia</i> species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Eastern rains												
<i>A. brevispica</i>	s				m	m	s					s
Summer dry season												
<i>A. bussei</i>									s	m	m	s
<i>A. etbaica</i>								s	m	m		
<i>A. reficiens</i>	s							s	m	m	s	s
<i>A. thomasii</i>							m	m	s		s	
Autumn rains												
<i>A. drepanolobium</i>	m	s			s	s	s					m
<i>A. nilotica</i>	m	s				s	s					m
<i>A. senegal</i>	m	s				s	s				s	m
<i>A. tortilis</i>	m	s					s	s				m
<i>A. zanzibarica</i>	m					s	s				s	m

1996–1997 (Table 2). Pollinator visitation was quantified in the same way for each *Acacia* species by watching the same set of 20 selected inflorescences for 30 minutes every 1–1.5 h through the day from before the onset of foraging until after it ceased. In our analysis, visitation is quantified in terms of the number of inflorescence visits made by each taxon. This measure is a more appropriate estimate of the value of the flower visitor to the plant (Horvitz and Schemske 1990) than an estimate of the forager population. Each visit to an inflorescence was given equal weight in estimating total visitation, regardless of the taxon making the visit, or the number of florets visited, or its duration. This is in part necessitated by the extremely rapid movements over inflorescence surfaces by some foragers. Differences in patterns of activity of foragers through time were analyzed using Kolmogorov-Smirnov tests (Sokal and Rohlf 1981). A more detailed analysis of differences in behavior of flower visitor taxa will be presented elsewhere (Stone et al., *unpublished manuscript*). Specimens of flower visitors were captured and identified at the Hope Department of Entomology, Oxford University, United Kingdom.

Similarities in floral visitation attributable to particular visitor taxa are quantified using proportional similarity (PS; Schoener 1970, Kephart 1983, Horvitz and Schemske 1990). For each comparison between two pairs of values (sites, days, species), PS was calculated as follows: (1) the proportions of the total number of inflorescence visits attributable to each visitor taxon were calculated for the two *Acacia* groups to be compared; (2) the modulus of the difference in proportions was calculated for each visitor taxon; (3)  $PS = 1 - 0.5$  (sum of the modulus values over all visitor taxa), where its value ranges from one (maximum similarity) to zero (no overlap whatsoever).

#### RESULTS

##### *The distribution of Acacia flowering patterns in seasonal time*

Months during which flowering by component *Acacia* species was observed are summarized in Table 3.

The highest diversity of flowering *Acacia* species in this habitat was present in December and January, following the autumn rains, when up to eight species flowered concurrently. In contrast to the majority of *Acacia* species, *A. thomasii* and *A. etbaica* flowered only during the dry season, at a time when very few individuals of other species were in flower. These species occupy seasonal flowering niches in which competition for pollinators with other *Acacia* species is either much reduced or avoided altogether.

##### *Intraspecific variation in diurnal timing of pollen release*

*Intraspecific variation at a single site on a single day.*—Intraspecific patterns of pollen release for *Acacia* species flowering together after the autumn rains are shown in Fig. 2. For all except *A. drepanolobium* (Fig. 2D), peaks for individuals of each species illustrated in Fig. 2 are significantly aggregated within the time period between dawn and dusk (*A. nilotica*  $V = 0.177$ ,  $P < 0.01$ ; *A. tortilis*  $V = 0.09$ ,  $P < 0.05$ ; *A. zanzibarica*  $V = 0.035$ ,  $P < 0.025$ ; *A. senegal*  $V = 0.028$ ,  $P < 0.025$ ). Intraspecific variation was lowest in the early morning dehiscence of *A. nilotica* and *A. tortilis* (Fig. 2A, B), and more marked in the later dehiscing *A. drepanolobium* and *A. senegal* (Fig. 2D, E). A different pattern was seen in *A. thomasii*, flowering alone in the dry season. The four *A. thomasii* trees sampled showed far more variation in patterns of pollen availability than any of the co-flowering species (compare Fig. 2 with Fig. 3A), with no statistical support for aggregated timing of pollen release. Means across trees showed no significant peak at any time period (Fig. 3B).

*Intraspecific variation among sites within a single season.*—Peaks of pollen availability in *A. zanzibarica* occurred at very similar times in all the sites sampled (Fig. 4A) and peaks of pollen availability across sites were significantly aggregated in time ( $V = 0.065$ ,  $P < 0.025$ ). Variation across sites was no greater than was

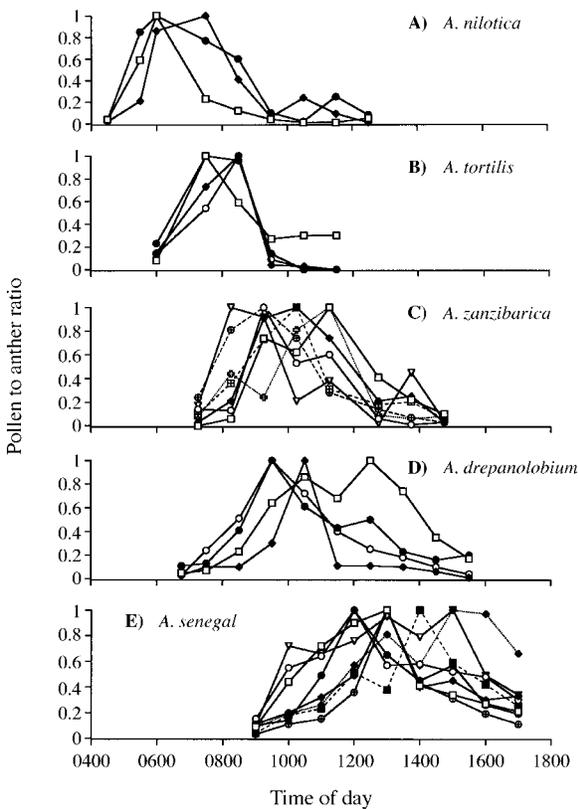


FIG. 2. Patterns of pollen availability through time for individual trees of *A. nilotica*, *A. tortilis*, *A. zanzibarica*, *A. drepanolobium*, and *A. senegal*. Each symbol type represents an individual tree.

found among individuals at a single site (Compare Fig. 2 with Fig. 4A). What differences there were in the timing of peak pollen availability between days at the same site, and among sites, were explained well by variation in relative humidity; peak pollen availability occurred later on days or at sites with a higher mean relative humidity over the period within which dehiscence was initiated (Fig. 4B).

Unlike *A. zanzibarica*, *Acacia senegal* showed no aggregation in timing of peak pollen availability among sites ( $V = 0.028$ ,  $P \gg 0.05$ ; Fig. 5A). Peak pollen availability occurred 2–4 h earlier at Zange and Vitiwini than at Kisima and Ubani, and the onset of dehiscence at Kisima was delayed relative to the other sites. Analysis of variance of the pollen-to-anther ratios indicates a significant difference between two pairs of sites (Zange and Vitiwini in one group, Kisima and Ubani in the other) over time (time  $\times$  group interaction term  $F_{8,125} = 2.6$ ,  $P = 0.012$ ). A possible explanation could be differences in daily patterns of microclimate between these pairs of sites: were a critically low value of relative humidity to be the cue for anther dehiscence, earlier peaks of pollen availability would be expected at sites whose relative humidity falls to this level earlier in the day. Zange and Vitiwini showed *earlier* anther

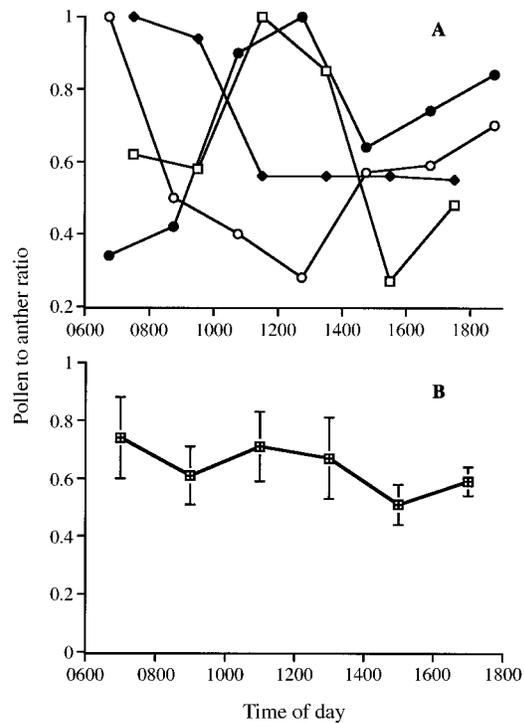


FIG. 3. Pollen release in *A. thomasii*. (A) Patterns of pollen availability through time for four individual trees (identified by different symbols in the figure) and (B) mean values over all four individuals ( $\pm 1$  SE) through time.

dehiscence despite *higher* relative humidity during the period preceding dehiscence (Fig. 5B), suggesting that some other difference between these populations is responsible for differences in the timing of pollen release. A consistent difference between the two pairs of sites is the presence/absence of *Acacia zanzibarica* in the co-flowering assemblage: early release in *A. senegal* coincides with absence of *Acacia zanzibarica* from Zange and Vitiwini, and later release coincides with presence of *A. zanzibarica* at Kisima and Ubani (Table 1).

*Intraspecific variation among flowering seasons and between years.*—Anther dehiscence in *Acacia nilotica* was recorded for the same trees in the autumn rains of 1995–1996 and 1996–1997 at the Ubani site, and for different trees at the Pangaro site following the Easter rains in 1996. In all three cases, flower opening and the onset of anther dehiscence took place before dawn, and there was no evidence of different patterns of pollen release either between years at a single site, or between flowering after the autumn and spring rains (Fig. 6A). Anther dehiscence was observed for the same individuals of *A. drepanolobium* (Fig. 6B) and *A. senegal* (Fig. 6C) over two successive autumn flowerings. For both species the agreement between the two flowering seasons is striking.

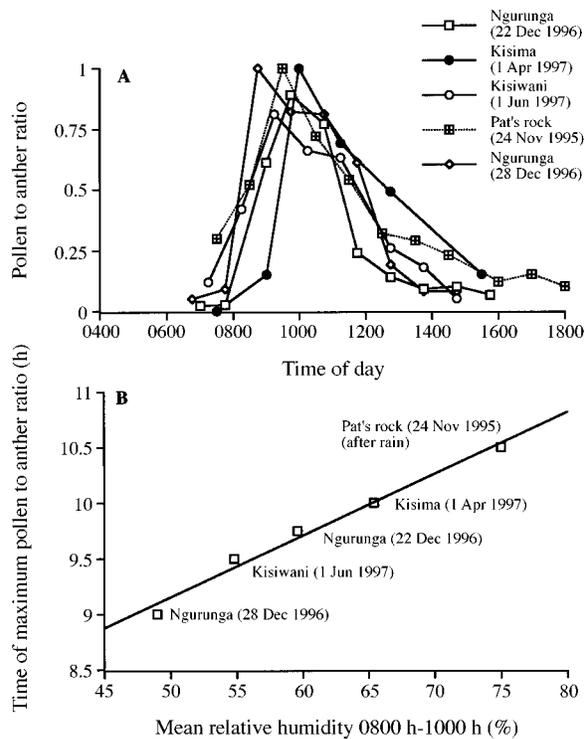


FIG. 4. (A) Intraspecific variation in patterns of pollen release over time between sites in *A. zanzibarica*. Data points are means over individual trees at each site. (B) Timing of maximum pollen availability as a function of mean relative humidity over the period 0800–1000 h for *A. zanzibarica*. The fitted line is a least squares regression with equation  $y = 0.055x + 6.381$ ,  $r^2 = 0.983$ ,  $P < 0.001$ .

#### Patterns in daily timing of pollen release across species

*Acacia* species that flower together during the autumn rains showed characteristic interspecific differences in daily timing of flower opening and pollen release (Table 4). *A. nilotica* and *A. tortilis* both opened their flowers well before dawn, and released their pollen at or shortly after sunrise. *Acacia drepanolobium* and *A. zanzibarica* flowers opened from 0700 h and began to release their pollen from 0800–0900 h. *A. bussei* released its pollen at a similar time to these two, but differed in that its flowers opened well before dawn and delayed anther dehiscence for 2–3 h. *A. senegal* flowers opened in mid- to late morning, and anther dehiscence followed immediately, giving peak availability during the middle of the day. Flowers of both *A. brevispica* and *A. reficiens* only began to open from 1100 h, and *A. brevispica* showed peak pollen availability in the afternoon. Although data on pollen release could not be collected for *A. reficiens*, the timing of flower opening means that peak pollen availability in this species must also occur in the afternoon.

Calculation of Williams' *V* shows that if all of the autumn rains *Acacia* species are included in the anal-

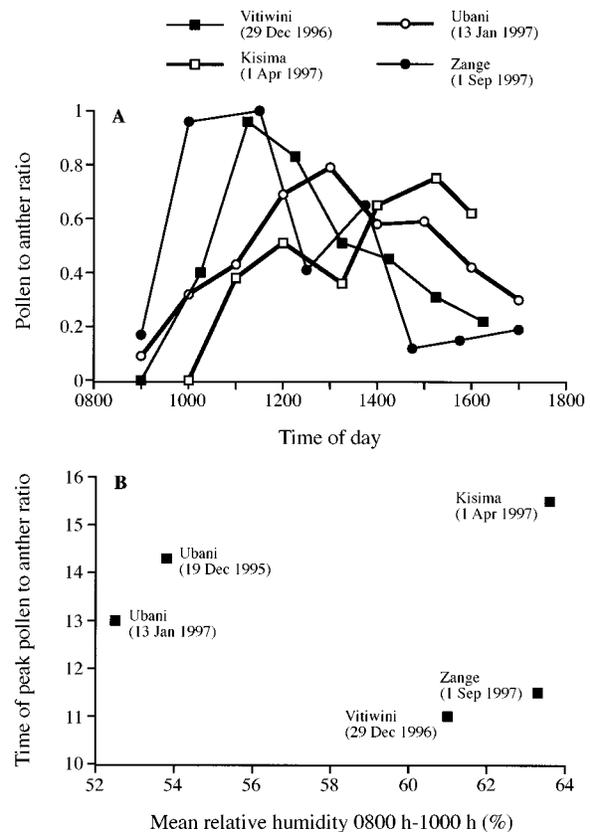


FIG. 5. (A) Intraspecific variation in patterns of pollen release over time between sites in *A. senegal*. Data points are means over individual trees at each site. (B) Timing of maximum pollen availability as a function of mean relative humidity over the period 0800–1000 h for *A. senegal*.

ysis there is no statistical support for significantly regular spacing of species peaks in daily pollen availability, either between dawn and dusk or between first and last species. Significant daily structuring is obtained in both types of analysis (Table 5A, B) if *A. drepanolobium* is excluded. We suggest that this is biologically justifiable, because as a specialist of black cotton soils this *Acacia* is rarely sympatric with other species. Significant structuring is also supported if the two other *Acacia* species whose membership of this co-flowering assemblage is least certain are excluded (*A. tortilis* because of soil preferences and *A. bussei* because of flowering seasonality) (Table 5A, B).

The influence of *Acacia brevispica* in our analyses shows how assumptions of the time resource being divided among species may affect the statistical support for temporal structuring. If spacing is analyzed between first and last species peaks (as for most analyses of seasonal phenology), significant structuring exists both with and without *A. brevispica* (Table 5B, C). If the resource to be divided is the period between dawn and dusk, however, significant structuring is supported only if *A. brevispica* is included.

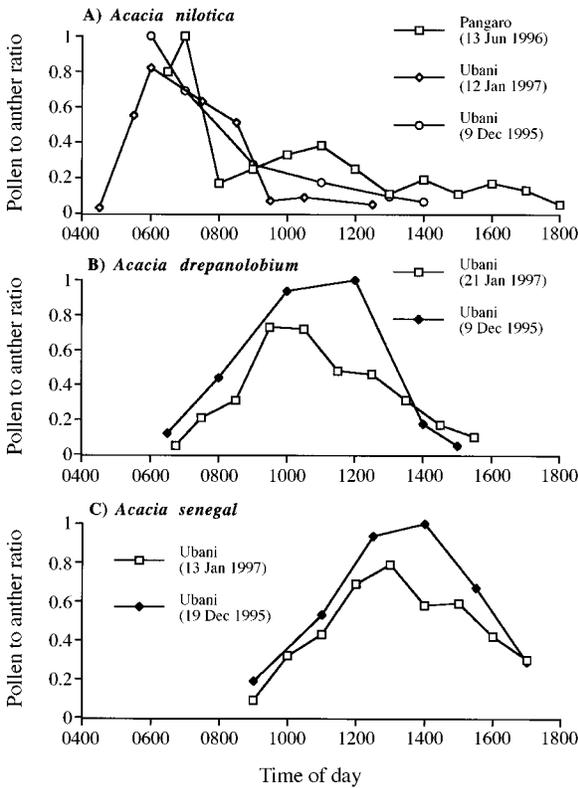


FIG. 6. Intraspecific variation in patterns of pollen release over time: (A) between years and between flowering bouts in a single year in *A. nilotica*, (B) between years for *A. drepanolobium*, and (C) between years for *A. senegal*.

*Do co-flowering Acacia species share pollinators?*

*Acacia senegal* is the only species in the sampled community to produce abundant nectar. Flowers contained their maximum volume of nectar (a mean of 1.35 ± 0.1 µL per floret at 19.8 ± 2.1% sucrose by mass) at the onset of dehiscence, and standing crop fell rap-

idly through visitation to reach barely detectable levels by noon. Nectar foragers consistently made up a high proportion of all visits to *A. senegal* (74–92%, Table 6A), including large, common, and highly mobile species of potential value as pollen vectors. Honey bees (*Apis mellifera*) were important visitors at two sites, and collected nectar only from *A. senegal*. Other visitors contributing significant visitation were nymphalid, papilionid, and pierid butterflies, anthophorine and megachilid solitary bees, pepsid spider wasps and two species of sunbirds (*Nectarinia hunteri* and *N. venusta*).

*Acacia tortilis* and *A. zanzibarica* flowers both produced minute quantities of highly concentrated nectar (<0.1 µL of >70% sucrose per floret; Stone et al. 1996) in comparison to *A. senegal*. Both species received substantial visitation from nectar foraging insects (Table 6B, C), including the same megachilid bees seen at *Acacia senegal*. Over a third of visits to *A. tortilis* were by small halictid bees foraging for nectar (Table 6E). The nectar foragers recorded at both *A. tortilis* and *A. zanzibarica* were mainly small species, without the larger nectar-feeding insects and sunbirds recorded from *A. senegal*. In contrast to *A. senegal*, both *A. tortilis* and *A. zanzibarica* received ~40% of their total daily visitation from a wide diversity of pollen-feeding flies, particularly syrphids of the genus *Eristalinus* and calliphorids of the genus *Rhyncomya* (Table 6B, C, E). *Acacia tortilis* received significant visitation from honey bees (*Apis mellifera*), which in marked contrast to their behavior at *A. senegal* at the same location only collected pollen at *A. tortilis*.

*Acacia nilotica* and *A. drepanolobium* produced no nectar, and almost no nectar foraging butterflies, wasps or honey bees were observed at flowers of either species (Table 6E). By far the most important visitors were megachilid solitary bees of the same species observed at *A. senegal*, *A. tortilis*, and *A. zanzibarica*. While *A. drepanolobium* received almost all of its visitation from

TABLE 4. Daily patterns of floral reward availability in the sampled *Acacia* species. Ellipses indicate that relevant data have not been collected. Values given for each variable indicate the ranges within species observed across days, sites, and years. Relative humidity at dehiscence represents the mean value over the period between onset of pollen release and maximum availability.

<i>Acacia</i> species	Nectar	Flowers begin to open (h)	Dehiscence begins (h)	Peak pollen availability (h)	Relative humidity at dehiscence (%)
<b>Subgenus <i>Acacia</i></b>					
<i>A. nilotica</i>	none	0200–0300	0400–0500	0600–0700	90–95
<i>A. tortilis</i>	trace	0400–0500	0600–0700	0750–0900	80–90
<i>A. drepanolobium</i>	none	0600–0700	0700–0800	1000–1200	60–70
<i>A. zanzibarica</i>	trace	0700–0800	0800–0900	1000–1100	55–65
<i>A. brevispica</i>	none	1000–1100	1000–1100	1500–1600	40–50
<i>A. reficiens</i>	...	1000–1100	...	...	...
<b>Subgenus <i>Aculeiferum</i></b>					
<i>A. bussei</i>	present	0400–0500	0700–0800	1000–1100	65–85
<i>A. senegal</i>	present	0900–1000	0900–1000	1100–1300	50–60
<i>A. thomasii</i>	...	throughout	throughout	no obvious peak	

TABLE 5. Values and significance of Williams' *V* for given *Acacia* assemblages and bounding assumptions. The letter "i" indicates that a given *Acacia* species is included in the series of peaks tested.

A) Assuming dawn–dusk limit to time axis							
<i>nilotica</i>	<i>tortilis</i>	<i>zanzi- barica</i>	<i>bussei</i>	<i>senegal</i>	<i>brevi- spica</i>	<i>V</i>	<i>P</i> value
i	i	i	i	i	i	0.00408	<0.025
i	i	i		i	i	0.00435	<0.025
i		i	i		i	0.00528	<0.025
i		i		i	i	0.00047	<0.001
B) Distribution of peaks between first and last in series, with <i>A. brevispica</i> included							
<i>nilotica</i>	<i>tortilis</i>	<i>zanzi- barica</i>	<i>bussei</i>	<i>senegal</i>	<i>brevi- spica</i>	<i>V</i>	<i>P</i> value
i	i	i	i	i	i	0.00710	<0.05
i		i		i	i	0.000	<0.001
C) Distribution of peaks between first and last in series, without <i>A. brevispica</i>							
<i>nilotica</i>	<i>tortilis</i>	<i>zanzi- barica</i>	<i>bussei</i>	<i>senegal</i>		<i>V</i>	<i>P</i> value
i	i	i	i	i		0.0067	<0.05
i		i		i		0.000	<0.001

a single megachilid bee species, *A. nilotica* at the same site were also visited by the same calliphorid and syrphid flies observed at *A. tortilis* and *A. zanzibarica*.

Similarity in patterns of visitation within and among *Acacia* species can be quantified with the proportional similarity (PS) statistic. All *Acacia* species showed intraspecific variation in their flower visitor assemblages. For all species, variation among sites (Table 7A, B) was greater than variation at a given site among days or years (Table 7C, D). Despite such intraspecific variation, differences in visitor taxa result in a gradient of proportional similarity values across *Acacia* species (Table 7E). *Acacia senegal* is most similar to *A. tortilis*, then *A. zanzibarica*, *A. nilotica*, and *A. drepanolobium*. This gradient correlates with differences among species in nectar production and is repeated for PS values for all of the pairwise comparisons among *Acacia* species.

Flower visitor assemblages in this *Acacia* community are thus characterized both by partial taxonomic partitioning and by overlap. Substantial differences in visitor guilds across *Acacia* species correspond to variation in the floral rewards available to foragers. *A. senegal* has a highly diverse assemblage of nectar-feeding insects, including large and mobile species, and the vast majority of visits by insects to this *Acacia* were for nectar. Conversely, flower visits to *A. drepanolobium* and *A. nilotica* were almost entirely for pollen, and there were very few visits by nectar-feeding insects. *Acacia* flower visitor assemblages nevertheless overlap. Megachilid solitary bees in the genera *Creightonella*, *Chalicodoma*, and *Megachile* visited all of the co-flowering *Acacia* species (Table 6A). Syrphid and calliphorid flies visited *A. nilotica*, *A. tortilis*, and *A. zanzibarica*, and honeybees were important foragers (though for differing resources) at *A. senegal* and *A. tortilis*.

#### *Is the activity of shared flower visitors structured by daily patterns of pollen availability?*

Temporal patterns of activity in the three groups of numerically significant flower visitors shared across *Acacia* species (megachilid bees, honey bees, and pollen-feeding Diptera) are described in turn.

**Megachilid bees.**—Megachilid bees arrived soon after dehiscence at each *Acacia* species and departed when pollen standing crop reached low levels, resulting in daily structuring of their activities that follows the sequence of dehiscence in the *Acacia* species. Megachilid bee activity at four co-flowering *Acacia* species at the Ubani site is shown in Fig. 7A. Although there was overlap of activity among *Acacia* species, all of the between-species differences are significant (Kolmogorov-Smirnov test,  $P < 0.001$  for all six pairs). Activity patterns of these bees at *A. tortilis* and *A. senegal* at Zange showed no overlap in time at all (Fig. 7B).

**Honey bees.**—At Zange honey bees visited *A. tortilis* for pollen and *A. senegal* for nectar. The distributions of activity at these two floral sources showed no overlap in time (Fig. 7B), and paralleled the timing of pollen release by the two *Acacia* species.

**Calliphorid flies.**—Activity by calliphorid flies showed significant differences among *Acacia* species at the Ubani site (Kolmogorov-Smirnov test,  $P < 0.001$  for all species pairs, Fig. 7C), and again tracked the sequence of dehiscence.

#### DISCUSSION

Four mechanisms contribute to structuring of flowering of sympatric *Acacia* species: spatial separation, seasonal separation of flowering in time, partial division of flower visitor assemblages, and daily patterning of pollinator behavior through timing of pollen release.

TABLE 6. Visitation by different taxa to *Acacia* species. Data are the percentage of total visits contributed by a particular taxon.

A) Variation between sites and years for <i>Acacia senegal</i>						
Site	Calliphorid flies	Syrphid flies	Megachilid bees	Other solitary bees	Honey bees	Wasps
Zange	1.3	†	12.4	37.2	44.4	2.1
Ubani 95–96	2.5	3.6	9.6	0.0	59.9	3.8
Ubani 96–97	†	†	7.9	3.7	86.4	†
Vitiwini	4.9	0.5	4.0	18.4	0.0	24.3
Kisima	9.7	†	15.8	58.0	0.0	6.1
B) Variation between days at a given site for <i>A. zanzibarica</i> at Pat's Rock						
Date	Calliphorid flies	Syrphid flies	Megachilid bees	Other solitary bees	Honey bees	Wasps
21 Nov 95	33.8	2.8	10.3	34.8	0	0
22 Nov 95	27.3	6.5	10	12.25	0	0
24 Nov 95	11.2	3.1	14.6	39.8	0	20
C) Variation between sites for <i>Acacia zanzibarica</i> . Mean values are used for the Pat's Rock site.						
Site	Calliphorid flies	Syrphid flies	Megachilid bees	Other solitary bees	Honey bees	Wasps
Pat's Rock	24.5	4.2	24.9	15.5	0.0	7.4
Kisiwani	22.7	†	21.7	34.0	0.0	21.7
Ngurunga	88.6	11.3	0.0	0.0	0.0	0.0
D) Variation between days at a given site for <i>A. nilotica</i> at Ubani						
Date	Calliphorid flies	Syrphid flies	Megachilid bees	Other solitary bees	Honey bees	Wasps
8 Dec 95	2.5	0.0	97.6	0.0	0	0
9 Dec 95	11.9	0.2	86.5	1.3	0	0
18 Dec 95	22.8	29.1	47.4	0.0	0	0
E) Comparisons between <i>Acacia</i> species in percentages of all visits contributed by particular visitor taxa ( $\pm 1$ SE).						
Species	Calliphorid flies	Syrphid flies	Megachilid bees	Other solitary bees	Honey bees	Wasps
<i>A. drepanolobium</i>	‡	0.0	98.0	0.0	1.3	‡
<i>A. nilotica</i>	12.0 $\pm$ 5.0	10.0 $\pm$ 0.8	76.0 $\pm$ 12.0	2.0 $\pm$ 1.0	0.0	0.0
<i>A. senegal</i>	4.1 $\pm$ 1.9	0.3 $\pm$ 0.1	10.1 $\pm$ 2.2	29.7 $\pm$ 10.2	33.1 $\pm$ 17.9	8.2 $\pm$ 4.8
<i>A. tortilis</i>	46.0	‡	8.3	34.1	11.1	‡
<i>A. zanzibarica</i>	40.7 $\pm$ 20.3	5.5 $\pm$ 2.7	17.7 $\pm$ 7.6	17.3 $\pm$ 7.25	0.0	12.0 $\pm$ 4.8

† Indicates <0.1% of total visitation per inflorescence over the entire activity period.

‡ Indicates a value between 0.0 and 1.0%.

#### Separation in space

Separation in space is the result of differing edaphic requirements of the component *Acacia* species, and in areas of homogeneous soil type this factor determines which species will characteristically be found together. As an extreme example, *A. drepanolobium* is the only *Acacia* capable of growing in soils that are seasonally waterlogged, and in extensive areas of such habitat there may have been little or no selection for the evolution of additional mechanisms preventing competition for pollinator visits or interspecific pollen exchange. Similarly, *A. thomasii* achieves considerable spatial separation through growing on hill slopes where few other *Acacia* species are found. However, where the habitat consists of a mosaic of soil types, *Acacia* communities characteristic of particular soil types

come into close proximity, and separation in space alone provides a poor barrier to interspecific pollen flow.

#### Temporal separation of flowering seasons

Partial structuring of flowering through separation of flowering season is apparent in this community, and there is no strong evidence in either *Acacia* subgenus of the phylogenetic similarity in flowering seasonality seen in some plant groups (Kochmer and Handel 1986, Johnson 1992, Wright and Calderon 1995). While a majority of species flower either predominantly or at least partially during the autumn rains, *A. brevispica* flowers predominantly after the Easter rains, and *A. bussei*, *A. etbaica*, *A. reficiens*, and *A. thomasii* flower during the dry season. These species thus do not in-

TABLE 6. Extended.

Lepidoptera	Percentage collecting nectar	Total visits per inflorescence	Total visits observed
†	86.3	86.3	604
20.6	90.0	23.9	357
1.5	92.1	46.9	352
45.7	90.6	141.7	992
10.1	74.5	29.3	278
Lepidoptera		Total visitation per inflorescence	Total visits observed
18.3		4.5	73
44.5		1.6	96
10.4		3.6	131
Lepidoptera		Total visitation per inflorescence	Total visits observed
23.4		3.25	100 ± 14
†		10.9	185
†		28.7	273
Lepidoptera		Total visitation per inflorescence	Total visits observed
0		16.1	370
0		14.4	446
0		5.1	127
Lepidoptera		Mean total visits per inflorescence	Mean total visits observed
‡		6.4	930
0.0		11.9 ± 3.3	314 ± 78
14.5 ± 9.3		76.0 ± 21.6	557 ± 139
‡		46.9	468
6.7 ± 5.2		15.8 ± 5.3	186 ± 41

teract with the diversity of species flowering during the autumn rains. *Acacia thomasii* achieves almost complete seasonal separation on rocky hill slopes in Mkomazi, with no other *Acacia* species flowering significantly in the same area at the same time.

#### *Interspecific differences in flower visitor assemblages*

Despite considerable spatial variation in the contributions to total visitation by particular visitor taxa, consistent differences in pollinator assemblages are generated by variation in the nectar rewards provided by *Acacia* species. Only *Acacia senegal* produces abundant nectar, thus monopolizing visitation by large nectar feeding butterflies, wasps, and sunbirds; these are probably efficient pollen vectors between trees (Waser 1982). *Acacia zanzibarica* and *A. tortilis* are also exploited as nectar sources, although at least some of the nectar visitors to these *Acacia* species are small and

rarely leave an individual tree (Stone et al., *unpublished manuscript*). Because all *Acacia* species studied to date are highly self-incompatible (Hocking 1970, Janzen 1974, Zapata and Arroyo 1978, Bernhardt et al. 1984) transport of pollen between individuals is probably essential, and it remains to be demonstrated that such local flower visitors contribute significantly to seed set (Thomson 1981, Rathcke 1988). Both *A. zanzibarica* and *A. tortilis* often grow in conspecific stands, and over short distances these nectar-feeding components of the flower visitor assemblages may be effective pollen vectors. *Acacia drepanolobium* and *A. nilotica* (and also, on the basis of limited data, *A. brevispica*) produce no nectar and depend almost entirely on pollen-foraging insects.

Division of available flower visitors among *Acacia* species is only partial, however. All the *Acacia* species for which visitation was studied shared three groups of specialist pollen-feeding flower visitors: syrphid flies, calliphorid flies, and megachilid bees. While the proportion of total visitation made up by these visitors varied across sites and species, the three together contributed from 10% (*A. senegal*) to >90% (*A. drepanolobium*, *A. nilotica*) of all flower visits. Their behavior during flower visitation suggests that the megachilids shared by *Acacia* species in this study are specialist pollinators and probably contribute more to *Acacia* pollination than our data suggest (Strickler 1979, Motten et al. 1981, Minckley et al. 1994, Stone et al., *unpublished manuscript*). The megachilid bees visiting *Acacia* (a) synchronize their arrival at an *Acacia* species closely with anther dehiscence, (b) collect pollen externally on a ventral scopa rather than in an internal stomach or crop, (c) collect quantities far in excess of the individual dietary requirements of a similarly sized insect, and (d) show higher rates of movement between trees than Diptera and Lepidoptera (Stone et al., *unpublished manuscript*). Their importance as pollen vectors is therefore almost certainly underestimated by simply counting the number of visits they make to each inflorescence (Beattie and Culver 1979, Motten et al. 1981, Waser 1982, Minckley et al. 1994, Willmer et al. 1994). In the absence of additional separating mechanisms, such shared visitors could contribute to mutually harmful interspecific pollen flow and may represent the selective force leading to the evolution of temporal partitioning seen in this community.

#### *Daily temporal partitioning of pollen release*

Daily temporal partitioning is predicted to result in intraspecific synchrony and interspecific divergence in timing of pollen release. Both of these patterns are supported in Mkomazi *Acacia* species that co-flower after the autumn rains. All but one of the co-flowering *Acacia* species showed significant intraspecific aggregation in timing of pollen release at a given site, and members of the same species show far less variation among sites, seasons or years than is present across

TABLE 7. Proportional similarities in levels of visitation by pollinator taxa for Mkomazi *Acacia* species, calculated from data in Table 3 using the formula given in the *Methods*.

A) <i>Acacia senegal</i> , across four sites in the autumn rains, 1996–1997			
Site	Ubani	Vitiwini Road	Zange
Kisima Road	0.13	0.44	0.54
Ubani		0.10	0.57
Vitiwini Road			0.26

B) <i>Acacia zanzibarica</i> , across three sites in the autumn rains, 1996–1997		
Site	Ngurunga	Pat's Rock
Kisiwani Road	0.23	0.67
Ngurunga		0.29

C) <i>Acacia zanzibarica</i> , across days for 21, 22, and 24 November 1995.		
Date	22 Nov 95	24 Nov 95
21 Nov 95	0.70	0.70
22 Nov 95		0.47

D) <i>Acacia nilotica</i> , across days for 8, 9, and 18 December 1995		
Date	9 Dec 95	18 Dec 95
8 Dec 95	0.89	0.50
9 Dec 95		0.60

E) Across <i>Acacia</i> species				
Species	<i>A. tortilis</i>	<i>A. zanzibarica</i>	<i>A. nilotica</i>	<i>A. drepanolobium</i>
<i>A. senegal</i>				0.11
<i>A. tortilis</i>			0.16	0.10
<i>A. zanzibarica</i>	0.53	0.47	0.22	0.18
<i>A. nilotica</i>		0.67	0.37	0.81

species. Across species, timing of pollen release ranges from dawn to mid-afternoon and, under plausible assumptions, peaks of pollen availability in the co-flowering assemblages are significantly regularly spaced.

While this result is compatible with character displacement among the co-flowering *Acacia* species, two factors urge caution in linking the observed pattern to this cause. First, as the example of *A. brevispica* shows, support for daily structuring is sensitive to the species included in the analysis. Because it is not known over what distance *Acacia* individuals and species may interact through shared pollinators, it is not intuitively obvious which species should be regarded as potential competitors (Armbruster 1986). Second, although we suggest it is unlikely, it remains possible that the observed temporal patterning results from ecological sorting of "preadapted" *Acacia* species, rather than character displacement (Armbruster 1985, 1986, Murray et al. 1987). Although patterns seen in *Acacia* must therefore be interpreted with caution, our data do suggest that daily time is a resource axis worthy of investigation, particularly where seasonal flowering phenologies are aggregated.

Two additional pieces of evidence support some role

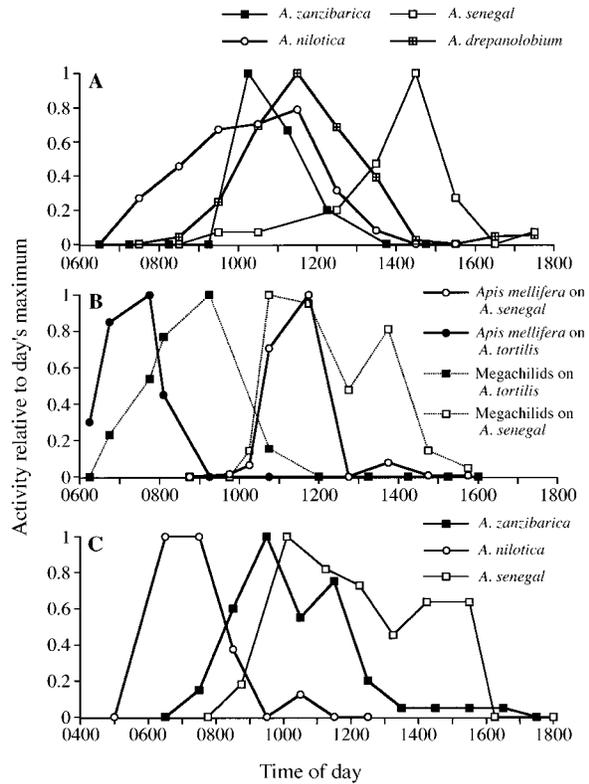


FIG. 7. Structuring of visitor activity through time across *Acacia* species for (A) megachilid bees at Ubani on 19 December 1995, (B) honey bees and megachilid bees at Zange on 10 January 1997, and (C) calliphorid flies at Ubani on 19 December 1995.

for interspecific competition in determining the temporal structuring of pollen release. First, *A. thomasii*, which flowers alone during the dry season, does not show the highly synchronized pollen release demonstrated by co-flowering species characteristic of the autumn rains. Although our small sample size precludes firm conclusions, one interpretation of this finding is that in the absence of competitors, *A. thomasii* has not been exposed to selection for mechanisms minimizing pollen exchange with other *Acacia* species, and exploits a far broader daily temporal niche for pollen release.

Second, there is some evidence that timing of pollen release in a single species is sensitive to local congeneric competition (Armbruster and Webster 1982, Armbruster 1985). *Acacia senegal* showed significant differences among sites in the timing of pollen release that correspond to differences in local *Acacia* community structure. Later dehiscence was recorded at sites where high densities of *A. zanzibarica* released their pollen between 0800 h and 1000 h. In contrast, early dehiscence was recorded at two sites (Vitiwini and Zange) without *A. zanzibarica* and with limited exploitation of the morning hours by other *Acacia* species. The earlier dehiscence of *A. senegal* at Zange and Vitiwini could thus be regarded as an example of competitive release

in the absence of *A. zanzibarica*. A possible selective pressure favoring earlier flower opening in *A. senegal* in the absence of *A. zanzibarica* may be a reduction in the metabolic cost of producing the large volumes of dilute nectar that recruit the majority of visitors to *A. senegal*. Earlier secretion of nectar by *A. senegal* may allow plants to invest water in nectar at a time when ambient relative humidity is higher and the plant is less water-stressed (Bertsch 1983, Nicolson 1993).

Further research is necessary to establish the significance of these differences in the timing of pollen release and their heritability. The differences in soil type underlying the differences in *Acacia* assemblage composition are long-lived features of the Mkomazi habitat, and the different associations between *A. senegal* and other species may thus have existed for long enough for evolution of local ecotypic variation to be a possibility. In particular, it would be useful to know the approximate scale on which *Acacia* populations are divided into genetic neighborhoods, and so the scale on which significant phenotypic differences may be maintained by low levels of gene flow (Turner et al. 1981). In zoophilous flowers long range gene flow is probably largely through pollen transfer by flower visitors (Levin et al. 1971, Schaal 1980, Schmitt 1980), although the dispersal distances of *Acacia* flower visitors in this habitat are unknown (for examples in other pollination systems see Visscher and Seeley 1982, Waser 1982).

We suggest that daily cycles of relative humidity may structure interspecific patterns of flower opening and anther dehiscence. The relationship between timing of anther dehiscence and relative humidity for *A. zanzibarica* suggests that pollen release occurs when a characteristic relative humidity is reached; a pattern well-established in the dehiscence of other plant structures (Grant 1996). The causal mechanism could be the drying of tissue in the anthers as relative humidity drops, resulting in splitting of the anther along lines of weakness (Meakin and Roberts 1990, Jenkins et al. 1996). Each of the *Acacia* species studied here released its pollen over a characteristic range of relative humidity (Table 4), and patterning across species could be generated by divergent selection on heritable variation in the relative humidity at which dehiscence is triggered. Such heritable variation is well established for other humidity-sensitive dehiscence mechanisms in plants (Grant 1996, Bailey et al. 1997).

#### *Interactions between temporal structuring of pollen release and activity of shared pollinators*

For interspecific variation in daily timing of pollen release to act as a mechanism restricting pollen transfer among *Acacia* species, activity of shared flower visitors must show corresponding temporal structure. Shared megachilid bees, honey bees, and pollen-feeding flies all show daily activity peaks across *Acacia* species at a location that track the daily sequence of dehiscence.

We suggest that separation of effective pollen transfer in time is more marked than counts of flower visitors would tend to suggest, because the first visitors to an *Acacia* after dehiscence will probably collect a higher relative proportion of total pollen released than later visits.

Several mechanisms may contribute to the ability of shared pollinators to track the daily sequence of pollen release in *Acacia* assemblages. Although we could not quantify it, dehiscence in each *Acacia* was associated with the release of strong, species-characteristic scents (undetectable from old flowers or buds) that may provide a synchronizing cue announcing the availability of a fresh standing crop in each species (Willmer and Stone 1997). Were *Acacia* floral scents to be concentrated in the pollen, as they are in some flowers (Dobson 1987), such a burst of scent would provide a genuine indication of resource availability detectable by both solitary and social bees (Lepage and Boch 1968, Dobson 1987). Second, in addition to odor cues, bees have a demonstrated ability to assess rates of pollen return while foraging (Buchmann and Cane 1989, Harder 1990), and so should be able to monitor the rapid decline in pollen standing crop observed at each *Acacia* species. An additional cue used by flower visitors to assess floral resource availability is floral color (Gori 1989, Weis 1991). We were unable to distinguish pollen-rich and pollen-free inflorescences on the basis of color, but changes may have occurred in ultraviolet wavelengths visible to insects. Whatever the cue(s) used by shared flower visitors, the observed structuring of their activity is thus compatible with foragers combining their sensory abilities to maximize daily pollen harvest (Stephens and Krebs 1991, Minckley et al. 1994).

#### *Wider significance of diurnal resource partitioning in flowering acacias*

Separation in seasonal time, space, or pollinator assemblages, and exploitation of separate regions on the bodies of shared pollinators are the four principal resource axes that have been discussed in the context of competition for pollination (Dressler 1968, Pleasants 1983, Rathcke 1983, Waser 1983, Ollerton and Lack 1992, Armbruster et al. 1994). Co-flowering *Acacia* species overlap substantially in all four, and by metrics applied to seasonal flowering phenology, should compete substantially (Pleasants 1980). Daily structuring of pollen release and shared pollinator activity, as described here and elsewhere (Armbruster and Herzig 1984, Armbruster 1985) provides two cautionary notes applicable to many existing studies of flowering phenology. First, the importance of a particular flower visitor in the pollination of a given *Acacia* species is very dependent on the daily time of observation. If all *Acacia* species in this study were watched only between 1100 and 1200 h each day, the daily structuring of shared pollinator activity would not be revealed, and

some important visitation in the system (almost all the visitation to *Acacia nilotica*, for example) would be missed entirely. Not only would differences among *Acacia* species in pollinator assemblages appear greater than they are, but the temporal structuring that may reduce competition within the system would not be detected. Second, estimates of the severity of competitive interactions among plant taxa based only on the degree of pollinator sharing and overlap in flowering seasons (Pleasants 1983, Rathcke 1983, Waser 1983) may need to be re-evaluated.

The demonstration of fine-scale daily partitioning raises a number of interesting questions. Predictions based on competitive explanations for phenological divergence in flowering seasons (Rathcke and Lacey 1985) can also be applied to daily partitioning. Just as species may diverge in flowering phenology (Rathcke 1983, Rathcke and Lacey 1985), so we might expect to find populations of a species in different competitive environments to diverge in their daily timing of pollen release. With the possible exception of *A. senegal*, we found little evidence of spatial variation in the timing of pollen release by the *Acacia* species in the community studied on a 20 × 50 km spatial scale. While *Acacia* species may be unable to respond to selection on this trait, a more probable reason is that our choice of sampling scale means that gene flow among populations prevented detection of local divergence. The possibility of significant intraspecific variation on a far larger geographic scale does exist for several of the *Acacia* species studied here. *Acacia nilotica*, *A. senegal*, and *A. tortilis* are widely distributed through Africa to Arabia and (for the first two species) India (Khan 1970, Ross 1981, Milton 1987, Coe and Beentje 1991), and form part of a wide diversity of *Acacia* assemblages with different pollinator guilds (Tybirk 1993). As yet, there are no data available on geographical variation in timing of pollen release.

Lastly, there has been considerable discussion of constraints that may act on flowering phenology (Kochmer and Handel 1986, Johnson 1992, Wright and Calderon 1995), and other constraints may act on daily timing of pollen release. Are there any phylogenetic constraints acting on daily timing of pollen release in *Acacia*? What characteristics of species (floral or otherwise) are associated with release of pollen at a particular time of day? Why do some *Acacia* species release their pollen around dawn, and others in the afternoon? Activity of bees and other insects can be strongly affected by daily microclimatic fluctuations (Willmer 1983, Herrera 1990, Stone 1994, Stone et al. 1995), and this may place constraints on the pollinators available to acacias flowering at particular times of day. Is there a best time to dehisce?

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