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5 December, 1996

Dear Ms Richardson,

MKOMAZI INVERTEBRATE DIVERSITY PROJECT

1. I thought you might like to see some recent ouputs from this project. The first is a publicity article from the Independant on Sunday and the second a paper on pollinator ecology by Dr Graham Stone, who was part funded by DI.

Yours sincerely,

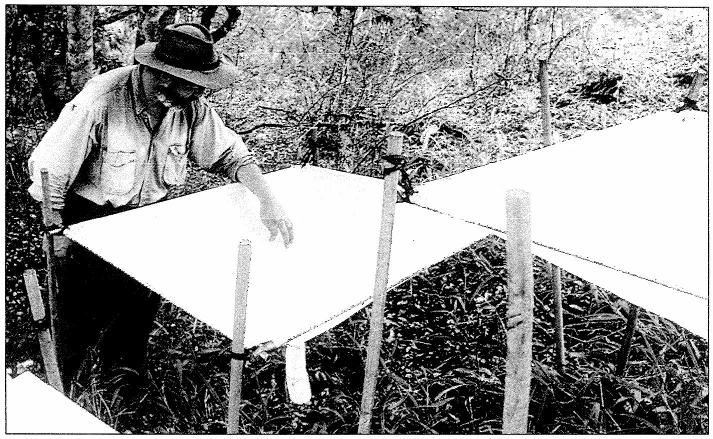
A. Russell Smith

Dr. A. Russell-Smith
Project Leader

Mr Tillson 9/12
For information
VR
9/12

3/248

GRASS ROOTS RESEARCH



GC MCGAVIN

Collecting a selection of the 70,000 animals that can inhabit a single tree in Mkomazi

Do savannahs teem with more life than the rain forests? **Matthew Brace** investigates

IN DR GEORGE McGavin's cluttered laboratory in Oxford's University Museum lie 1,000 specimen tubes. They cover his workbench, swarm around his microscope and huddle together in plastic bags under his desk.

Each vial contains hundreds of insects. Such is their number that Dr McGavin, a leading entomologist and the assistant curator of the museum, is expecting to be working overtime ploughing through the lengthy backlog of analysis to be done. This is the latest batch he has carried back to his Oxford lair from an area of seemingly barren, and previously unstudied, East African savannah that is yielding a remarkably abundant insect fauna.

In fact, Dr McGavin and his fellow scientists working in the Mkomazi Game Reserve in north-eastern Tanzania believe they have discovered an ecological treasure chest, an area more diverse than many rain forests, in terms of the numbers of arthropods (animals with segmented bodies and jointed appendages – insects, spiders, centipedes, etc). On an average day, after "mist-blowing" a tree in the reserve with insecticide, Dr McGavin watches as clouds of insects fall from the branches into his collection trays. During years of research in rain forests, deserts and grasslands around the world he has never seen such abundance.

"When I first started working out here I was amazed," he said. "Each morning I'd rush out with my collecting gear knowing I'd be coming back laden with insects at the end of the day."

If Mkomazi is representative of other unstudied areas of savannah in East Africa, these discoveries could go some way to challenging the traditional belief that rain forests are the richest habitats on Earth.

"When people are asked about diversity they always think about rain forests," says Dr McGavin. "Savannahs might have fewer species than rain forests but according to our results in Mkomazi, the numbers of individual insects are immense. In that sense, the savannahs are more diverse [scientifically diverseness is not just richness of species but also abundance]."

His preliminary examinations of 15 acacia trees (from two species, *Acacia zanzibarica* and *Acacia tortilis*) show that the average arthropod specimen count is 1,600 per square metre. One small tree can hold more than 70,000 individuals. The major rain forest canopy arthropod studies of the past 12 years have produced much smaller specimen totals. Similar studies have confirmed the relative arthropod diversity of the grasslands. The highest figure in the Toraut lowland forest of Sulawesi, south east Asia, was 461 per square metre; dry evergreen tropical forest in north-east Thailand yielded between 123 and 256 per square metre; and subtropical rain forest near Brisbane, Australia, registered just 34 per square metre. Although it is unlikely Mkomazi will compete with rain forests on overall species richness (the number of different species), the reserve is continuing to reveal a surprisingly large variety of species, some of which are presently undescribed.

While he has identified roughly 500 known species in these two acacia types, Dr McGavin estimates from his early results that one in five of the arthropods from the acacias is unidentified, or, new to science. These new arrivals will help swell the list of the million-plus species of known insects, which make up 56.3 per cent of all living organisms.

And it is not just the plethora of insects that is putting Mkomazi on the diversity map. Entomologist and principal scientific officer at the National Resources Institute, Dr Tony Russell-Smith, has logged 575 morpho-species (species yet to be finally catalogued) and estimates up to 20 per cent will turn out to be new to science.

> ANTS COMSUME FAR MORE ANIMAL TISSUE THAN THE BIG ANIMALS, IT'S JUST THAT YOU DON'T SEE THEM DOING IT

However, it is the number of spider families represented in Mkomazi that has stunned Dr Russell-Smith. "There are between 150 and 200 known spider families, in the tiny area we have been looking at – about 850sq km – we have discovered at least a quarter of that total."

The intense sampling methods used by both Dr McGavin and Dr Russell-Smith could account for some of the high results they have been recording, but neither is in any doubt that in Mkomazi they have found an area of remarkable ecological diversity and value.

Another main faunal survey, of birds, has resulted in one of the highest bird counts ever in East Africa. Dr Peter Lack, head of information systems at the British Trust for Ornithology, has identified roughly 400 species.

"Mkomazi is one of the most diverse areas ever found," says Dr Lack. "And these high bird counts are important from a conservation point of view as they allow us to learn how these systems work and how we can preserve them."

So why such abundance? One main reason is Mkomazi's geography. The reserve lies at the southern end of the great East African savannah – a continuation of the Tsavo system over in Kenya. Within the reserve's 3,600sq km are various different environments – pockets of forest, areas of water, and a range of wooded hills called the Pare mountains. It is this variety that allows Mkomazi to support many species.

Before this project little work had been done in the area, according to Dr McGavin. "We know so little about savannahs but are always striving to study the rain forests, about which we know relatively much more," he said. "I'm not knocking rain forests – they are wonderful things – but the concentration of efforts on them detracts from other areas. Hopefully, the incredible diversity this reserve is revealing will show that savannahs need to be understood so they can be protected if necessary."

He added: "Tropical grasslands cover about one sixth of the world's land. Although we now understand them in terms of the big animals we certainly don't understand them in terms of the small ones. But insects are crucial to this environment. They shape it, they make the savannah system work. Ants, for example, carry off and consume far more animal tissue than the big animals – it's just that you don't see them doing it because they are so small."

The research in Mkomazi is part of an ongoing programme co-ordinated jointly by the Royal Geographical Society (with the Institute of British Geographers) and the Tanzanian Department of Wildlife.

The Society got involved when the Tanzanian government (condemned as the reserve has lost much of its game and been ravaged by fires), came to them in 1989 for help in undertaking a major geographical study of the area in order to collect information to prepare a long-term management plan for the future of the reserve.

The programme has remained an Anglo-Tanzanian venture with joint directors Mr Bukari Mbano, director of wildlife in the Tanzanian Ministry of Natural Resources and Environment, and Dr Malcolm Coe, a leading ecologist from St Peter's College, Oxford.

The project won a Darwin initiative grant worth more than £100,000 to fund work to describe, in quantitative terms, the diversity of the terrestrial invertebrate fauna of Mkomazi and to assess the influence upon it of natural and human-induced factors.

And the significance of the work has been recognised by organisations including Friends of Conservation, the British Council, BA, Land Rover, and BP which have contributed towards the £250,000 sponsorship of the project.

The project recently secured a further initiative grant and the possibility of making Mkomazi a long-term field study is being discussed. Such a plan would keep a window constantly open on what is turning out to be one of the most exciting areas for biodiversity research. □

Daily partitioning of pollinators in an African *Acacia* community

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SUMMARY

Many studies have shown sympatric plants with similar floral structures to have flowering periods separated in time, and this is usually interpreted as a selective response to competition for pollination. In highly seasonal habitats, however, the time available for flowering may be highly constrained, and many species often flower together. Under such conditions, one alternative to temporal partitioning on a seasonal scale is for species to flower simultaneously, but with pollen release (dehiscence) structured on a diurnal timescale. Here we provide evidence for such diurnal partitioning of both floral resources and pollinator visitation in an African *Acacia* community. Temporal separation is enhanced by differences in the rewards offered by *Acacia* species to their pollinators: species producing nectar as well as pollen receive flower visits from insect groups absent from acacias offering only pollen. In contrast to competition for pollination, this situation may promote mutualistic maintenance of shared pollinators by the *Acacia* species.

1. INTRODUCTION

Competition for pollination among sympatric flowering plant species is thought to be an important force structuring plant communities (reviewed by Pleasants 1983; Rathcke 1983; Waser 1983; Kochmer & Handel 1986; Widén 1991). Fitness reduction for competitors may result from loss of pollen, clogging of limited stigmatic surface with allospecific pollen and, for animal-pollinated plants, competition for pollinator visits. Though sympatric species are unable to diverge in space, they may use different pollinator guilds (Armbruster & Herzig 1984; Rathcke 1988). Where pollinator guilds overlap significantly, time remains a resource which may be partitioned between species. Many studies have shown sympatric plants with similar floral structures to have flowering periods separated in time, and this is usually interpreted as a selective response to competition for pollination. Separation of flowering seasons as a result of competitive displacement is predicted to result in a distribution of species flowering peaks that are regularly spaced (over-dispersed) through time (Poole & Rathcke 1979; Pleasants 1983; Williams 1995).

In many ecosystems the temporal axis along which partitioning may occur is tightly constrained. In highly seasonal habitats, from arctic tundras to tropical savannahs, plant species often flower together over a brief period (Janzen 1967; Hocking 1968), thus limiting the potential for avoidance of competition through temporal separation on a seasonal timescale. An alternative for plants which share pollinators and which are constrained to flower simultaneously is a finer division of the pollinator resource over a diurnal timescale. Thus the plants may appear to flower simultaneously, but species differ in the time of day at which dehiscence takes place. As for seasonal partitioning, competitive displacement is predicted to result in regular spacing of species' timing of pollen release through the day (Williams 1995). Although suggested as a possibility (Levin & Anderson 1970; Ollerton & Lack 1992), there are very few examples of such daily partitioning (Armbruster & Herzig 1984).

We present evidence for this phenomenon in an *Acacia* community in a highly seasonal savannah habitat in Tanzania. Acacias (Leguminosae; Mimosoideae; genus *Acacia*) are dominant in many arid and semi-arid African ecosystems (Ross 1981), and most flower for relatively brief periods after seasonal rainfall (Ross 1981; Tybirk 1989; Coe & Beentje 1991; Tybirk 1993). More than ten species may grow in close proximity and several species often bloom together. Furthermore, *Acacia* flowers are grouped into easily accessible inflorescences, resulting in a degree of overlap in guilds of flower visitors across *Acacia* species (Tybirk 1989, 1993). The flowering species thus overlap in space, time and in their flower visitor guilds. How then do they avoid competition for pollination?

We examined the patterns of daily pollen and nectar release, and flower visitation by insects, in four sympatric, simultaneously flowering *Acacia* species. These form a natural community with a long evolutionary history (Ross 1981) and it is thus reasonable to use adaptive reasoning to interpret any observed patterns. Given that these species are sympatric and coflowering, and are thus unable to avoid competition for pollination in space and seasonal time, we ask whether there is any evidence for community structuring on a finer, diurnal, timescale. To this end, we address two sets of questions.

1. Do *Acacia* species differ in their timing of reward release through the day in a manner consistent with competitive displacement? Is there any response by flower visitors to plant-driven temporal patterning?

2. Do *Acacia* species differ in the nature of reward offered to flower visitors? Is there any evidence of reward-driven divergence in the flower-visiting guilds?

2. METHODS

(*a*) *The study site*

This study was done during November and December 1995 in the Mkomazi Game Reserve in northern Tanzania. The study area consists of *Acacia-Commiphora* bush at an altitude of approximately 1000 m with a highly seasonal pattern of rainfall. The main rains fall in November and December, with a second and more diffuse period from April to early June.

(*b*) *The* Acacia *species studied*

In Africa there are two subgenera of *Acacia*: flowers in the subgenus *Aculeiferum* often secrete nectar and are typically borne on elongated inflorescences, while those in the subgenus *Acacia* they are usually nectarless and borne in spherical inflorescences. The flowers of both subgenera are typically protandrous, and last for a single day (Tybirk 1989, 1993). The study community contained four acacia species; *A. nilotica* (L.), *A. zanzibarica* (S. Moore) and *A. drepanolobium* Sjöstedt in the subgenus *Acacia*, and *A. senegal* (L.) Willd. in the subgenus *Aculeiferum*. Cross-pollination is obligate for many acacias, including *A. drepanolobium* (Hocking 1970), and in others seed set through self fertilization is much reduced relative to outcrossing (see, for example, Tybirk 1993). All of the species discussed here set seed during the study period, and the outcome of pollen transfer at this time is thus of selective importance. This aspect of the system is discussed further elsewhere (P. Willmer *et al.* unpublished data).

(*c*) *Nectar secretion, anthesis and flower visitors*

Individual flowers consist of a narrow corolla tube occupied by many filaments (Tybirk 1993; G. Stone *et al.* unpublished data). Presence or absence of nectar was determined with a 1 μl micropipette (Camlab, U.K.) drawn out to a fine point. Nectar volume was determined from the length of the nectar column in the micropipette. Nectar concentration was measured using a hand-held refractometer specially modified for very low volumes (Bellingham & Stanley, U.K.).

Pollen release (anthesis) in each species was quantified using the relative abundance of pollen available on the inflorescence surface at intervals through the day. Each inflorescence (sampled once only) was rolled lightly across the adhesive side of a piece of clear adhesive tape, which was then placed over a slide and examined with a microscope. The progress of anthesis over time was recorded by scoring the ratio of anthers to polyads (compound pollen grains common to all acacias) collected on the tape. Before anthesis, only unopened anthers were collected. Once anthers began to dehisce, polyads were also collected, numbers increasing as dehiscence took place, and then decreasing as they were removed by flower visitors. For each *Acacia* species, three inflorescences were sampled from each of two trees at each sample time through the day. For each inflorescence, the ratio of anthers to polyads was recorded for five different microscope fields and the mean calculated. For each time interval, pollen supply is expressed as the pollen to anther ratio averaged over three inflorescences per tree and over two trees per species.

Pollinator visitation was quantified by watching selected inflorescences for set time intervals (minimum 30 min) through the day. Specimens of flower visitors were captured and identified at the Hope Department of Entomology, Oxford University.

(*d*) *Statistical methods*

A number of methods have been developed to test temporal partitioning between flowering species, all of which test the null hypothesis that species' blooming periods are randomly distributed through time. Here we use the *Var* statistic, *V*, proposed by Poole & Rathcke (1979) and shown to be the only suitable existing statistic for detecting competitive displacement (Pleasants 1994; Williams 1995). Significant values of *V* reject the null hypothesis given above, and show that flowering periods are significantly regularly spaced, or overdispersed, in time. The flower visitors observed at acacias were all diurnal species, and we thus assume that the time axis available for division between visitors is restricted to daylight hours. The null hypothesis tested is that the peaks of pollen availability are randomly distributed between dawn and dusk.

3. RESULTS

(*a*) *Patterns of reward provision by the Acacia species*

(*i*) *Anther dehiscence is structured in time*

Acacia nilotica, *A. zanzibarica*, *A. senegal* and *A. drepanolobium* flowered together during the study period, but differed in their daily pattern of pollen release (figure 1*a*). *A. nilotica* flowers opened during the night, and anthesis occurred before dawn. *A. zanzibarica* flowers opened around dawn and were followed by *A. drepanolobium*, both species completing dehiscence between 10h00 and 12h00. Flowers of *A. senegal* began to open between 7h00 and 9h00, reaching full anther dehiscence by 14h00. Timing of anther dehiscence for each *Acacia* was consistent across days.

Between dawn and dusk, pollen availability maxima were more regularly spaced than would be predicted by chance alone ($V = 0.0058$, $p < 0.05$; Williams 1995), supporting the resource division hypothesis.

(*ii*) Acacia *species differ in the rewards available to foragers*

Only flowers of *A. zanzibarica* and *A. senegal* were found to produce nectar. In *A. zanzibarica* the nectar volumes secreted per flower were very small, and a summed collection from ten flowers gave a concentration of ca. 75 % sucrose. This nectar was nevertheless

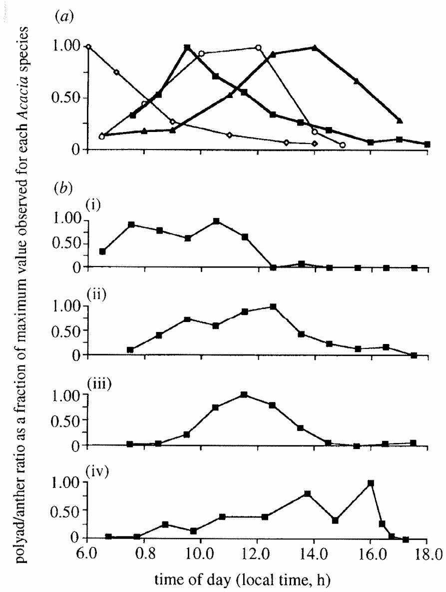

Figure 1. Resource availability and pollinator activity in the *Acacia* community. (*a*) Pollen release and removal through time for the four *Acacia* species. Pollen availability was measured using the ratio of polyads (compound pollen grains) to anthers, which increases as anthers dehisce and pollen becomes available, and then falls as pollen is removed by flower visitors. Data for each species are made compatible by expressing values as proportions of the maximum seen in each species. Points joined by heavy lines are for *Acacia* species producing nectar as well as pollen. Key to figure: square = *A. zanzibarica*; circle = *A. drepanobolobium*; diamond = *A. nilotica*; triangle = *A. senegal*. (*b*) Pollinator visitation through time for the four *Acacia* species. Activity is scored using summed visits by pollinators in 30 min observation intervals of 20–30 inflorescences per *Acacia* species on days of observation in December 1995. Data for each species are made compatible by expressing values as proportions of the maximum seen in each species. (i) *A. nilotica* (pollen only); (ii) *A. zanzibarica* (nectar and pollen); (iii) *A. drepanolobium* (pollen only); (iv) *A. senegal* (nectar and pollen).

accessible to foragers. A female nomiine bee observed collecting *A. zanzibarica* nectar was induced to regurgitate its load, producing 5 μl of nectar with a sucrose concentration of 78%. This is very close to the concentration recorded in the flowers.

A. senegal is the only species in this community to produce abundant nectar. Nectar volumes were highest soon after flower opening, and fell from 1.3 ± 0.1 μl per flower, (mean $\pm$ 1 standard error, $n = 10$) at 07h00, to 0.20 ± 0.06 μl, ($n = 19$) at noon. Over the same period, nectar sucrose concentration rose from a mean of $16.75 \pm 0.6\%$ to $63.4 \pm 5.4\%$.

The sequence of anther dehiscence across species, and the distribution of nectar production among the acacias in this community, mean that through the day there is an alternation of pollen-only acacias with pollen-and-nectar acacias (figure 1*a*).

(*b*) *Insect visitors to flowers*

(*i*) *Flower visitation to* Acacia *species is partitioned in time*

Insect visitation to *Acacia* flowers is summarised in table 1, and the distribution through time of pollinator visits to observed flowers is shown in figure 1*b*. Data on pollen loads and forager activity suggest that most of the pollen transfer is mediated by bees (G. Stone *et al.*, unpublished data). The summed activity of pollinators at each *Acacia* species clearly follows the temporal separation between species in pollen release (figure 1*a*). This is most clearly seen by comparing *A. nilotica* and *A. senegal*. *A. nilotica* shows early morning dehiscence, and insect activity at this species is negligible after noon. *A. senegal* showed dehiscence from 09h00–13h00, and insect activity at this species peaks in the afternoon. *A. drepanolobium* and *A. zanzibarica* both show dehiscence and forager activity in the middle of the day, and so overlap extensively in time. In all four *Acacia* species, pollen removal by foragers is rapid, with 75% of maximum recorded availability removed over a period of 3 h (figure 1*a*). Different visitor taxa showed similar temporal patterns, suggesting that whichever vistors are acting as pollinators the structuring of visitation in time will remain.

(*ii*) *Nectar secretion recruits additional visitor taxa*

There are clear differences in the visitor guilds associated with the species producing only pollen (*A. nilotica* and *A. drepanolobium*) and those producing additional nectar (*A. zanzibarica* and *A. senegal*) (table 1). The two pollen-only species received the most (78–98%) of their visits from solitary bees and very few or no visits from butterflies, beetles, honeybees or nectar-feeding wasps (table 1).

Nectar production (even of very small volumes in the case of *A. zanzibarica*) resulted in significant numbers of flower visits by nectarivores (table 1). In both *A. senegal* and *A. zanzibarica*, ca. 20% of all visits were made by nectar-feeding Lepidoptera and 5–10% by nectar collecting wasps. Approximately 61% of all floral visits to *A. senegal* were made by nectar-collecting honeybees (*A. mellifera*) which visited none of the other *Acacia* species under study. While insect populations may fluctuate widely between seasons, and the importance of particular species as pollinators may vary from year to year, these differences in flower visitor guilds are striking. The differences in the rewards offered by acacia species will remain from year to year, suggesting that the observed differences in associated guilds will themselves be consistent.

There is thus partial separation between acacias on the basis of visitor guild. The alternation of pollen-only and pollen + nectar flower types through the day means that the temporal separation between nectar-dependent components of the visitor guilds is further enhanced. Differences in the reward offered mean that the two species showing greatest temporal overlap in pollen availability (*A. zanzibarica* and *A. drepanolobium*, figure 1*a*) differ substantially in which insects visited them.

Table 1. *Summary of visitation data for the four* Acacia *species observed in November and December* 1995

(Data are records over whole days of activity, representing a single day for *A. senegal* and *A. drepanolobium*, and means over three days (± 1 s.e.) for *A. zanzibarica* and *A. nilotica*. To simplify interpretation of the data, values of less than 0.1 (table a) or 1 (table b), are indicated by an asterisk (*), and values of 0 by a dash.)

(*a*) *Total numbers of visits received by an inflorescence through the entire activity period*

	butterflies	muscid flies	syrphid flies	beetles	honey bees	solitary bees	wasps
A. senegal	2.0	0.3	0.4	0.1	6.8	1.1	0.44
A. zanzibarica	0.6 ± 0.1	0.8 ± 0.3	0.1 ± 0.02	0.14 ± 0.02	–	1.5 ± 0.05	0.25 ± 0.2
A. drepanolobium	*	*	–	*	0.1	6.3	*
A. nilotica	–	1.1 ± 0.3	0.5 ± 0.4	–	–	10.3 ± 3.3	–

(*b*) % *of visits by different visitor groups*

	butterflies	muscid flies	syrphid flies	beetles	honey bees	solitary bees	wasps
A. senegal	18	2	4	*	62	10	4
A. zanzibarica	22 ± 6	23 ± 5	4 ± 1	6 ± 2	-	38 ± 8	7 ± 5
A. drepanolobium	*	*	–	*	1.3	98	*
A. nilotica	–	12 ± 5	10 ± 8	–	–	78 ± 12	–

(*iii*) *All four* Acacia *species share some visitor guild members*

Some flower visitors are common to all four *Acacias*, and in the absence of temporal structuring of pollen release there would thus be potential for interspecific pollen transfer. The principal shared components are several solitary bees of the genera *Megachile*, *Creightonella* and *Chalicodoma* in the family Megachilidae. Of these, a single small *Megachile* species was dominant, and made ca. 80% of all flower visits to *A. nilotica*, almost all flower visits to *A. drepanolobium*, 9% of visits to *A. senegal* and 1–2% of visits to *A. zanzibarica*. Megachilid bees are known to be important pollen vectors in African (Tybirk 1989, 1993) and Australian (Bernhardt 1987) acacia communities, and it is thus possible that their presence as a shared guild component may provide a selective force for temporal partitioning. Species other than *A. drepanolobium* also shared several fly species in the families Syrphidae and Calliphoridae which contributed a significant proportion of all flower visits (see table 1).

(*iv*) *No single* Acacia *species monopolises flower visitation*

Despite differences in the timing and nature of the reward offered to flower visitors, the total number of visits received by an individual inflorescence through its reproductive life was relatively constant across species, ranging from 3.5 in *A. zanzibarica* to 11.9 in *A. nilotica* (see table 1). No single species thus had a monopoly of forager visits to its flowers.

4. DISCUSSION

(*a*) ***Resource partitioning in the*** **Acacia** ***system***.

Overlap of flowering in space and seasonal time, structurally similar and accessible flowers, overlapping visitor guilds and inability to monopolise forager activity all predict that mechanisms reducing competition for pollination should have adaptive value in this acacia community. Our data provide the clearest example yet of avoidance of such competition through diurnal temporal partitioning among a group of congeneric plant species. Pollen release by the four acacias is structured through the day, and insect visitors respond to this structure. Even were the taxonomic distribution of flower visitors to vary markedly between years (see, for example, Willmer *et al.* 1994), similar temporal patterns across visitor taxa suggest that the overall diurnal patterning would remain. Pollen standing crops in each species were rapidly removed, such that through migration of pollinators between acacias each achieved a similar rate of flower visitation. Flower visitors such as bees are known to be sensitive to floral reward availability (Frankie & Haber 1983; Buchmann & Cane 1989) and transfer of foraging between acacias through the day is thus to be expected. Solitary bees collect discrete pollen loads and then remove almost all of the pollen collected on return to the nest. Bees which are shared between acacias whose anthesis is separated in time will thus collect a series of pollen loads through the day in which each *Acacia* species in turn is dominant. Transfer of pollen between species must therefore be substantially reduced in comparison to a situation in which all four species release their pollen simultaneously. Intraspecific genetic variation in flowering times has been demonstrated (Widén 1991) and there seems no reason to doubt that selection could result in the temporal structure seen in this system.

Temporal partitioning is reinforced by partitioning of the available visitor fauna resulting from differences in floral rewards (Armbruster & Herzig 1984; Rathcke 1988). The nectar-producing species received a substantial proportion of their total visitation from insects absent from the guilds of the pollen-only acacias. *A. senegal* produced abundant dilute nectar, and received a high proportion of all flower visits from nectar-foraging honeybees. Despite the overall similarity in flower structure in the other *Acacia* species, honeybees were never observed to visit them. *A. zanzibarica*, in the section *Acacia*, is not predicted to produce nectar by its taxonomic position (Ross 1981), and yet the small quantities of concentrated nectar produced had a significant effect on its visitor guild.

Not all interactions between coflowering plants are negative: plants flowering together may sustain high pollinator populations and mutually facilitate pollination (Rathcke 1983). Flowering species separated through time may maintain pollinators in which individuals are long lived or have several generations each year (sequential mutualism, Waser & Real 1979). This acacia system may well result in simultaneous mutualism, by facilitation of pollination through maintaining rapid reproduction of pollinators over the short period for which growth and resources are available.

(*b*) *The significance of daily temporal structuring for studies of other plant communities*

Considerable effort has gone into the statistical testing of the distribution of flowering seasons in plant communities. All such community datasets show varying degrees of overlap in the flowering seasons and minimization of this overlap is the assumed goal of temporal resource partitioning. The ecological inference from such analyses is that species which overlap entirely through their seasons would compete throughout that period.

Our study shows that even where two species flower on the same days over the same season and share the same pollinators, competition inferred in this way may be virtual rather than real. If species do show significant diurnal separation of flowering times, then even if they share pollinators and overlap in flowering seasons it must be erroneous to include them all in an analysis of seasonal flowering phenology. Data for plant species which in fact avoid competition through diurnal separation may well have influenced previous analyses of flowering seasons. Very few studies of seasonal phenology provide the information on floral biology required to assess whether plant community members are in fact potential competitors, and we encourage future analyses to take fine partitioning of the temporal resource into consideration.

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