# Multi-species pollination interactions in a Kenyan savannah ecosystem

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# Abstract

Previous work on African acacias has shown that co-flowering species (those that flower in the same place at the same time) partition the activity of shared pollinators, and so avoid competition for pollination. The main aim of this thesis is to assess the evidence for temporal structuring of pollinator activity at a second African site, Mpala, in north central Kenya. I address this issue both for a guild of acacia species, and go beyond previous work to examine daily temporal patterning at the level of flowering communities. This second approach involves the generation of pollination webs for different periods of time within a single day, and the use of null modelling to compare temporal structure in real and randomised visitation data. I replicated this approach over sites and seasons, and generated the first pollination webs for any African savannah habitat.

Analysis of patterns within acacias requires identification of sets that co-flower, and so could potentially compete for pollination. Analysis of a long term dataset (1999-2005) revealed extensive co-flowering across Mpala acacia species, but little consistency in co-flowering species across years and sites. Previous work in Tanzania found co-flowering acacias to show high synchrony in timing of daily pollen release, and significant overdispersion (regularity in spacing) of species pollen release peaks through the day. This pattern is as predicted for the partitioning of a resource (shared pollinators) along a resource axis (daily time) by competitive displacement. Activity of shared pollinators tracked pollen release across the co-flowering acacias, resulting in partitioning of pollinator activity within the acacia assemblage. In contrast, I found Mpala acacias to show relatively low intraspecific synchrony in dehiscence. Further, although species' pollen release peaks ranged through the day between dawn and dusk, their distribution showed no significant signature of competitive displacement.

Mpala acacias share visitor species, particularly bees and syrphid flies. Visits to flower heads tracked the timing of pollen availability, illustrating the potential for 'bottom-up' influences in this system. Thus, whilst coflowering Mpala acacias could potentially partition shared pollinators in daily time through divergence in the timing of dehiscence, no evidence for such a mechanism was found. Possible reasons for absence of such a pattern at Mpala are discussed.

I quantified flower-visitor interactions for two replicate flowering communities at four seasonal time points in 2004. Flowering plant species, visitor species and the interactions between them varied through seasonal time and between sites. Mpala acacias shared visitors with many other plant species, illustrating the value of adopting a community perspective. A novel null-modelling approach found all seasonal datasets to show significant daily temporal structure, resulting from concentration of activity by specific groups of flower visitors within a subset of the four daily time periods sampled. Consideration of patterns of floral resource provision in specific plant taxa (e.g. Malvaceae) showed that at least some of this temporal structuring was the result of 'bottom-up' control. My data were not adequately resolved to assess community-wide evidence for partitioning of shared pollinators, but the presence of temporal structure means that this remains a possibility. Further work is required to assess the potential of 'top-down' influences (such as bee nesting cycles or visitor thermal physiology) in structuring daily temporal patterns. The significance of my results for other types of interaction webs is discussed.

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# Table of Contents

# Chapter 1. General introduction

The majority of angiosperms rely on animal pollinators to mediate pollen transfer from anthers to stigmas to enable successful fertilisation (Buchmann and Nabhan 1996, Proctor et al. 1996). Interactions between plant and pollinator species are usually beneficial for both parties. Whilst plants receive assistance with reproduction, pollinators obtain a reward provided by the plant. In most cases the reward is in the form of nectar and/or pollen, which both have a nutritive value for the pollinator. Other rewards, such as floral oils or protection from predators, are provided by some plants (Faegri and van der Pijl 1979, Proctor et al. 1996).

Plant species that flower together in space and time or 'co-flower' have the potential to interact negatively or positively for pollination. Plants that have a negative impact on the pollination of sympatric species are usually competing for visits by the same pollinators. Species can also positively affect neighbouring plant species' reproductive success and this has been termed 'facilitation' (Rathcke 1983). I will discuss these processes in more detail later in this chapter (Sections 1.1-1.3).

Plant species can minimise negative competitive interactions by partitioning pollination between them along a resource axis. Several axes along which this occurs have been studied, namely (i) use of different pollinators (e.g. Heinrich 1976, Pleasants 1980), (ii) using different body regions of the pollinator (e.g. Dressler 1968, Yang et al. 2007), (iii) segregation in space (e.g. Armbruster and Herzig 1984), (iii) segregation in seasonal time (e.g. Stiles 1977, Aizen and Vazquez 2006), and (v) segregation in daily time (e.g. Armbruster and Herzig 1984, Stone et al. 1996, 1998, Raine 2001). Axes (ii) through to (v) would only be necessary if plant species shared pollinators. Partitioning of pollination along these axes will be discussed in more detail in section 1.1.

Of these axes, divergence in daily time has received the least attention. Daily pollinator partitioning has been shown for two species of *Dalechampia* (Armbruster and Herzig 1984), and one multi-species plant guild (Stone et al. 1996, 1998). In the latter study the timing of pollen release (dehiscence) for six co-flowering acacia species in Tanzania was significantly regularly spaced in daily time, and visits by shared pollinators closely tracked patterns of pollen availability in each species. Raine (2001) found evidence for a similar process among acacia species in Mexico.

The extent to which divergence in daily time as a potential mechanism for avoiding competition is found among co-flowering species assemblages is unknown. Given that it has been demonstrated for one group of acacia species, is the structuring of pollinator visits in daily time found for other groups of acacia species? Furthermore, should examination for this mechanism be extended beyond groups of closely related plant species in a given plant community? In this thesis I examine the evidence for daily temporal partitioning within two groups of flowering plant species: (i) a multi-species acacia assemblage and (ii) entire flowering plant communities.

I will now discuss a number of issues in more detail that are relevant throughout the thesis.

## 1.1 Competition for pollination

*(a) Mechanisms of competition for pollination*

Competition for pollination is thought to be an important force structuring flowering plant communities (reviewed in Pleasants 1983, Rathcke 1983, Waser 1983, Feinsinger 1987). Competition between plant species for the same pollinators can have a negative impact on the reproductive success of individual species and may lead to the divergence in character traits among species that minimises competitive overlap. This will be discussed in more detail in section (b).

Competition for pollination refers to an interaction among sympatric flowering plants in which the use of shared pollinators depresses reproduction. Two types of reproductive disadvantage can result for plant species sharing pollinators (Waser 1978a, b, Rathcke 1983):

(i) **Competition for pollinator visits**: One plant species can draw pollinators away from another resulting in less pollen transfer between individual plants for the second species (e.g. Free 1968, Mosquin 1971, Lack 1976, Bierzychudek 1981, Horvitz and Schemske 1988, Rathcke 1988b). This could lead to lower levels of pollination which in turn might affect seed set and overall reproductive success.

(ii) **Competition for pollen quality**: Heterospecific pollen transfer can occur when pollinators forage on multiple plant species (e.g. Waser 1978a, Campbell and Motten 1985, Waser and Fugate 1986, Feinsinger and Tiebout 1991, McLernon et al. 1996, Murcia and Feinsinger 1996). This can result in the deposition of pollen on a stigma of the wrong species and could affect reproductive success in several ways (reviewed in Wilcock and Neiland 2002). Firstly, pollen will be lost by the donor species. Secondly, heterospecific pollen can inhibit successful fertilisation by conspecific pollen through (a) reducing the space available for conspecific pollen, (b) interfering with pollen germination or tube growth or (c) causing the loss of receptivity to conspecific pollen (Waser and Fugate 1986, Murphy and Aarsen 1995, McLernon et al. 1996). The deposition of heterospecific pollen on the stigma of a closely related species could also lead to fertilisation resulting in hybrid offspring and a loss in fitness for both species (Klips 1999).

Both of these processes can lead to pollination limitation, resulting in a decrease in seed set and reproductive success (see Knight et al. 2005). However, plants can potentially achieve adequate or maximum seed set even with loss of pollinator visits and deposition of heterospecific pollen (see section 1.2).

### *(b) Resource axes along which plant species can diverge to avoid competition for pollination*

An expected evolutionary consequence of competition is the divergence of species along some resource axis (resource partitioning) to reduce the negative interaction between coexisting species (Brown and Wilson 1956, Pianka 1974, Schoener 1983). Five resource axes along which plant species partition pollination have been investigated:

1. Recruitment of different pollinator species
2. Utilisation of different body regions of a pollinator for pollen transport
3. Segregation in space
4. Segregation of flowering in seasonal time
5. Segregation of pollinator activity in daily time

**Axis 1.** Sympatric co-flowering plant species can recruit different pollinators (e.g. Heinrich 1976, Inouye 1978, Pleasants 1980, 1983, Armbruster and Herzig 1984, Rathcke 1988a, b, Muchhala 2006). Pleasants (1980) found that different groups of plants in meadow communities recruited different bumblebee species as pollinators. Often specialised floral morphologies can allow plants to partition pollinators. For example, Heinrich (1976) showed that different co-flowering plant species were visited by different bumblebee species according to tongue length; long tongued bees visited flowers with longer corolla tubes and shorter tongued bees visited flowers with shorter corolla tubes. Several species are entirely dependent on a 'private pollinator' that visits no other plant species. Examples of this include fig wasps (see review by Cook and Rasplus 2003) and yucca moths (see review by Pellmyr 2003).

**Axis 2.** Plant species flowering at the same seasonal time can reduce competition for the same pollinator species by placing pollen on discretely different parts of a pollinator's body for pollen transport (Dressler 1968, Armbruster et al. 1994, Yang et al. 2007). This requires co-adaptation between floral morphology and that of the pollinator to achieve accurate pollen placement and retrieval (Brown and Kodric-Brown 1979). This kind of pollinator partitioning is found in certain orchid species that attach discrete packets of pollen (pollinia) to specific locations on their pollinators, male euglossine bees (Dressler 1968). Yang et al. (2007) found that two species of *Pedicularis* sharing a bumblebee pollinator, *Bombus richardsi*, deposited pollen on different parts of the bumblebee, the locations of which corresponded to those contacted by the stigma of the appropriate species during foraging.

**Axis 3.** Plants sharing pollinators could utilise independent populations of the same pollinator species through separation in space (Pleasants 1980, Armbruster and Herzig 1984, Rathcke 1988b). Flight distances and foraging ranges of pollinators will determine the degree of spatial separation necessary to avoid interspecific pollen transfer. Armbruster and Herzig (1984) found that although two vine species, *Dalechampia dioscoreifolia and D. tiliifolia*, shared euglossine bee pollinators, they usually occurred in different habitats. Where they occurred sympatrically, interspecific pollen transfer was considerable and seed set was depressed in *D. discoreifolia*.

**Axis 4.** Plants growing in the same location that share pollinators can diverge in their seasonal timing of flowering (e.g. Stiles 1977, Waser 1978a, Pleasants 1980, Kephart 1983, Ashton et al. 1988, Petanidou and Vokou 1993, Rocha et al. 2005, Aizen and Vazquez 2006). In this way, plant species can use the same pollinators at different times of year, therefore avoiding competition for pollinator visits and decreasing the risk of interspecific pollen transfer. Stiles (1977) demonstrated that flowering peaks for ten species of plants pollinated by hermit hummingbirds were staggered in seasonal time in a Costa Rican rainforest. Aizen and Vazquez (2006) showed that the flowering phenologies of plant species pollinated by the hummingbird *Sephanoides sephaniodes* were significantly regularly spaced in seasonal time at three sites in Chile and Argentina. An assumption of past work on seasonal partitioning has been that plants flowering at the same seasonal time may compete for pollinators.

**Axis 5.** Sympatric species that share pollinators and flowering seasons could partition pollinator visits in daily time. Divergence among co-flowering species in the timing of pollen release (dehiscence) through the day could reduce the potential for competition in two ways (Levin and Anderson 1970). Firstly, the structuring of pollen availability in daily time could result in the daily partitioning of pollinator behaviour, so that co-flowering plants avoid competition for pollinator visits. Second, since many pollinators remove pollen from their body at regular intervals (Roubik 1989), temporal partitioning of their activity will result in pollinators carrying predominantly one type of pollen at any one time, thus reducing interspecific pollen transfer.

Few studies have examined pollinator partitioning on a daily timescale. Armbruster and Herzig (1984) first found evidence of daily pollinator partitioning between two species of *Dalechampia* at a site in Panama. *Dalechampia heteromorpha* and *D. scandens* grew in the same location, flowered together for a significant portion of the year, and were visited by the same bee pollinators in the genera *Hypanthidium* and *Trigona*. Examination of dehiscence time and flower visitation patterns in these species revealed that *D. heteromorpha* dehisced at 7.00 and was visited by bees in the morning, whereas *D. scandens* dehisced at 13.30 and was visited by the same bee species in the afternoon.

Stone et al. (1996, 1998) found evidence of pollinator partitioning in daily time for a group of co-flowering acacia species in Tanzania. The timing of dehiscence for six acacias was significantly regularly spaced between dawn and dusk, and flower visits by shared megachilid bees and calliphorid flies closely tracked the pollen availability of each species such that each acacia species received pollinator visits in turn throughout the day, with little overlap. Raine (2001) found evidence for a similar mechanism among two co-flowering acacia species in Mexico. Two co-flowering acacia species dehisced at different times of day, with shared pollinators corresponding closely to maximum pollen availability, resulting in little overlap in pollinator activity.

## 1.2 Tolerance of competition for pollination

Co-flowering plant species that share pollinators can sometimes show no obvious means by which competition is avoided. Even if there are sufficient pollinators for all species, there will still be a risk of interspecific pollen transfer. Divergence along resource axes to minimise competition may not be possible due to climatic constraints (e.g. timing of wet and dry seasons) or limited pollinator diversity. Lower reproductive success resulting from competition for pollination could be tolerated when the disadvantages of competition are smaller than the disadvantages of diverging along a resource axis. For example, a disadvantage of divergence in seasonal time could be flowering at a suboptimal time for pollinators. It is also possible that the apparently detrimental effects of reduced pollinator visits or interspecific pollen transfer might have no effect on the level of seed set by a plant. There are several reasons why plants might be able to tolerate competition for pollination:

(i) Self-compatible plants can self-pollinate as long as heterospecific pollen does not prevent access to the stigma. Such species would have no need to develop mechanisms to reduce competition as pollination could be achieved without pollinator visits. However, self-pollinated plants could experience decreased seed set in comparison to those receiving pollen from another individual (e.g. Rathcke 1988b).

(ii) Species with long lived flowers might be able to tolerate competition for pollination as seed set could occur with even small numbers of pollinator visits (Primack 1985, Motten 1986, Rathcke 1988a, b, 2003). By producing flowers that are open for longer than those of competitors, plant species can increase the chance of pollinator visits after competing species cease flowering, or when pollinators are scarce (Rathcke 2003).

(iii) Heterospecific pollen deposited on stigmas can interfere with stigma receptivity or pollen tube growth; however some plant species have been found to be tolerant of heterospecific pollen deposited on stigmas (e.g. Motten 1986).

### 1.3 Facilitatory interactions for pollination

Pollination facilitation occurs when the presence of one species increases pollinator visitation to another species, at no cost to either species (Rathcke 1983). Facilitation can occur in two ways:

(i) The combined resources of several plant species can support the survival and reproduction of pollinators throughout the season and from year to year (Waser and Real 1979, Rathcke 1983). Waser and Real (1979) suggest that sequential flowering of the species *Delphinium nelsonii* and *Ipomopsis aggregata* helps to maintain shared hummingbird pollinators, and that facilitation is a consequence of divergence of seasonal flowering times.

(ii) Plant species can act together to attract larger numbers of pollinators. Character convergence for pollinator sharing could arise between species if facilitative interactions are effective (Rathcke 1983). Brown and Kodric-Brown (1979) suggested that a community of hummingbird-pollinated plant species producing red tubular flowers had converged in their floral characteristics. They argued that the advantages of using similar signals and rewards to share the same pollinators outweighed the disadvantages of diverging to reduce interspecific competition. Schemske (1981) suggested a similar process for two species of *Costus* that are identical in flower morphology and patterns of nectar secretion and share a euglossine bee pollinator. He suggested that low floral densities for both *Costus* species increased effective flower density and nectar supplies for pollinators and probably increased pollinator visitation rates.

## 1.4 Considerations of competition and resource partitioning

### 1.4.1 Patterns of species dispersion along resource axes

Divergence among plant species along the resource axes listed in Section 1.1 can reduce the negative interaction between coexisting species and hence the effects of interspecific competition for pollination. This divergence is termed character displacement (Brown and Wilson 1956). Character displacement between species along a resource axis can result in resource partitioning. The resource being partitioned along the resource axes described in Section 1.1 is pollinator visits to flowers.

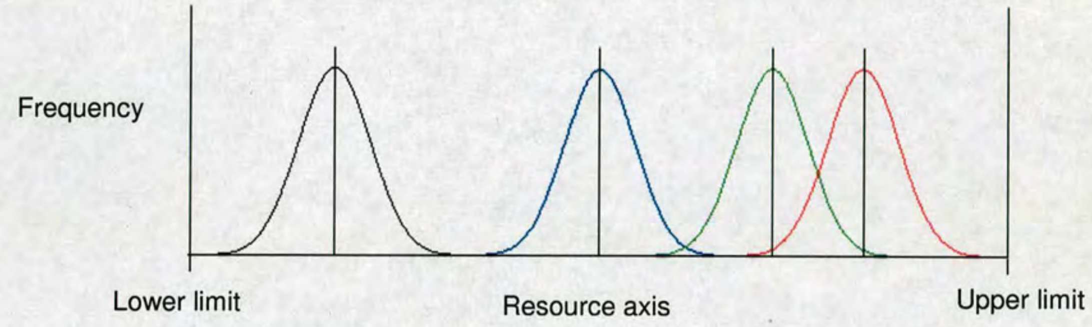
Species which have diverged in a particular character trait (e.g. timing of seasonal flowering) due to interspecific competition are expected to be regularly, rather than randomly, spaced along a resource axis (see Fig. 1.1). This regular spacing is also known as 'overdispersion'. The process of divergence along a resource axis occurs as a result of intraspecific variation in resource usage becoming restricted by the negative effects of interspecific competition in the overlapping region of the shared resource axis. Resource partitioning through interspecific competition requires long-term community stability to allow divergence of resource use through consistent directional selection acting on both competing species over an evolutionary timescale.

### 1.4.2 Detecting resource partitioning due to interspecific competition

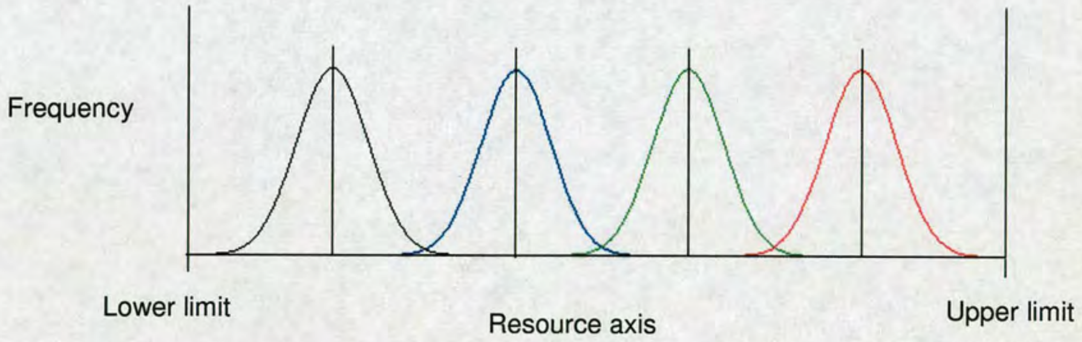
If interspecific competition has caused divergence between species along a resource axis, we expect: (i) intraspecific synchrony and (ii) interspecific divergence in patterns of resource use along a shared resource axis. Visual inspection of the distribution of resource patterns is not sufficient to identify the regular spacing of species along resource axes such as seasonal flowering time or daily time of dehiscence. Various statistical methods have been developed for detecting character displacement of species' traits due to interspecific competition (Poole and Rathcke 1979, Pleasants 1980, 1994, Williams 1995).

Poole and Rathcke (1979) proposed the first suitable statistic for testing character displacement. Their statistic, *P*, was developed in order to test whether the midpoints of the flowering seasons of plant species sharing pollinators were regularly spaced in seasonal time. Pleasants (1994) considered *P* the most appropriate statistic with which to detect character displacement since it has more statistical rigour than alternatives. Williams (1995) developed the *V* statistic, an improved version of *P*, and also provided a table of critical values that can be used to test both one tailed and two tailed hypotheses.

(a) Species randomly dispersed



(b) Species regularly spaced or overdispersed



(c) Species distributions aggregated

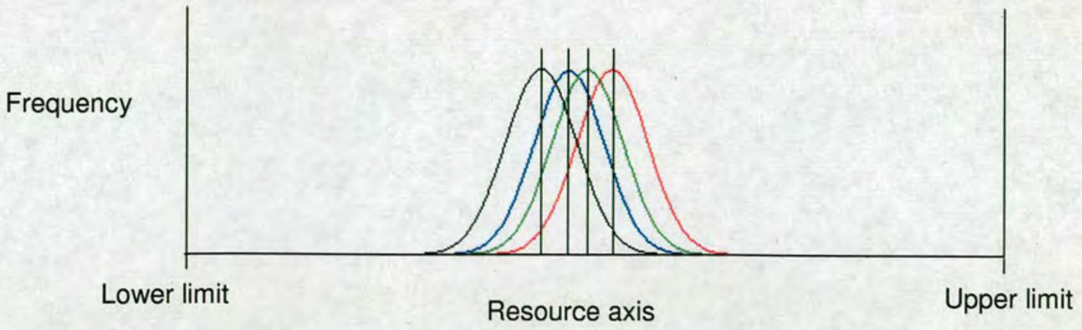


Figure 1.1 Potential distributions of species along a resource axis. Each curve represents variation within a single species around a species mean. (a) shows species that are randomly dispersed along a resource axis, (b) shows species that are regularly spaced along the same axis and (c) shows species that are aggregated.

In a two-tailed test, the *V* statistic compares the observed distribution of resource utilisation among species with a null prediction that the patterns of resource use by members of a hypothetical assemblage, containing the same number of species, are randomly distributed along a given axis. The null hypothesis will be rejected if species values are either more regularly spaced or more aggregated than expected by chance within a defined range, when *V* has a significance smaller than 0.025 or greater than 0.975 according to Williams' (1995) table of critical values. Two types of one tailed test can be used to test two different null hypotheses:

(i) That species values are not regularly spaced along a resource axis, with an alternative hypothesis that species values are more regularly spaced than expected by chance. The null hypothesis will be rejected for values of *V* with a significance smaller than 0.05.

(ii) That species values are not aggregated within a resource axis, with an alternative hypothesis that species values are more aggregated than expected by chance. The null hypothesis will be rejected for values of *V* with a significance greater than 0.95. This test could also be used to test whether individuals of the same species are more aggregated than expected by chance.

Therefore the *V* statistic can be used to test both of the predictions for resource partitioning due to character displacement: intraspecific synchrony and interspecific divergence.

For a given set of species means along a resource axis, calculation of *V* requires an estimation of (i) the distances between successive species (or individuals when examining intraspecific synchrony within a single species) and (ii) the range within which the dispersion of the species should be measured. *V* is then given by the expression:

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

The *V* statistic can be used to detect character displacement among plant species. However, demonstration that the shared resource (i.e. shared pollinator visits) also follows the same sequence of species is also necessary to demonstrate resource partitioning.

### 1.4.3 Detecting character displacement and resource partitioning in daily time

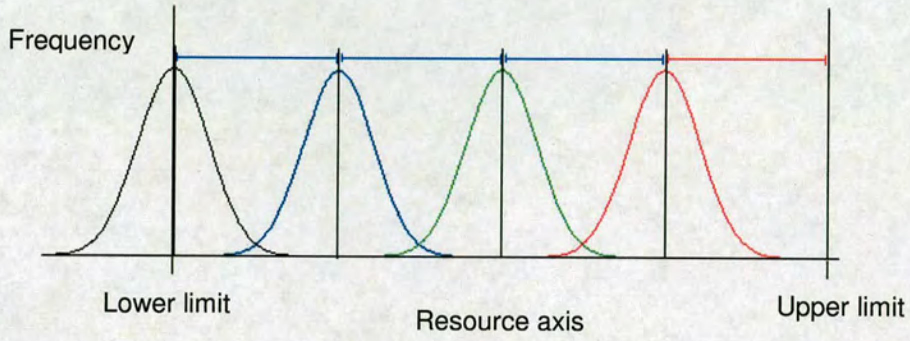
Poole and Rathckes' *P* statistic was originally developed to test the dispersion of species' flowering peaks in seasonal time. Stone et al. (1996, 1998) used Williams' (1995) *V* statistic to test for evidence of character displacement among the times of daily maximum pollen availability for a group of co-flowering acacia species sharing pollinators in Tanzania. If sharing pollinators is costly for co-flowering acacia species, it is expected that (i) members of the same acacia species will overlap as much as possible (intraspecific synchrony) and (ii) members of different acacia species will overlap as little as possible (interspecific divergence) in both pollen availability and pollinator visits in daily time. Stone et al. (1996, 1998) used one tailed tests of the *V* statistic to examine the evidence for intraspecific synchrony and interspecific divergence in the timing of maximum pollen availability. In this community the mean values for co-flowering acacia species were significantly regularly spaced in daily time and individuals of each species showed high levels of synchrony. These results provide evidence of character displacement in the timing of dehiscence among co-flowering acacias in this community. Since shared pollinators tracked the patterns of pollen availability between species this is compatible with the theory of resource partitioning in daily time.

In this thesis I use the *V* statistic in the same way to test for evidence of character displacement in the daily times of maximum pollen availability among co-flowering acacia species in a Kenyan savannah community.

I will now explain some of the issues associated with using the *V* statistic in this context. One of the difficulties in using the *V* statistic is determining an appropriate resource axis range within which to test the dispersion of species means. When testing for divergence in seasonal time, previous studies have taken the range as the distance between the first and the last species in the sequence (Poole and Rathcke 1979, Prescott 2005). This is the only approach where there are no *a priori* limits to the resource axis between which species should be dispersed, i.e. we cannot say that species can only flower between specific dates for physiological, phylogenetic or other reasons. This approach has also been applied to tests of species' pollen availability peaks in daily time (Stone et al. 1998) and is appropriate if pollinators could potentially visit flowers at any time of day or night. However, data to date suggest that all significant pollinators visit acacia flower heads during the day (between dawn and dusk) in East Africa (Tybirk 1989, 1993, Stone et al. 1996, 1998, this thesis). In Tanzania the earliest acacia species dehisced at dawn (6.00) and the latest at 15.00, therefore Stone et al. (1998) also calculated the *V* statistic between dawn (6.00) and dusk (18.00). In this thesis I similarly examine the distribution of pollen availability peaks in daily time between both the first and last peaks of pollen availability and between dawn and dusk.

The incorporation of a specific resource axis range can be important because it adds additional values to analyses. Incorporating dawn and dusk as limits in daily time increases the number of gaps between 'species' as the limits are included in the analyses. Figure 1.2 shows two examples of species distributions in daily time, and demonstrates how using different ranges could affect the results of a test using the *V* statistic. In analyses of daily partitioning, the last available species 'slot' for pollen release is not at dusk, but a period before dusk that allows visitation by diurnal pollinators. In Fig 1.2a the species are regularly spaced between the first and last peaks and between dawn and dusk. However, in Fig 1.2b the species are regularly spaced between the first and last peaks, but aggregated between dawn and dusk. Therefore the range used can have a major impact on results expected using the *V* statistic. In analyses of intraspecific synchrony, the range will need to encompass values before the first species and after the last species (Fig. 1.2b) in order to be able to detect aggregation within a specified time limit.

(a) Species regularly spaced between first and last peaks, and between dawn and dusk



(b) Species regularly spaced between first and last peaks, but aggregated between dawn and dusk

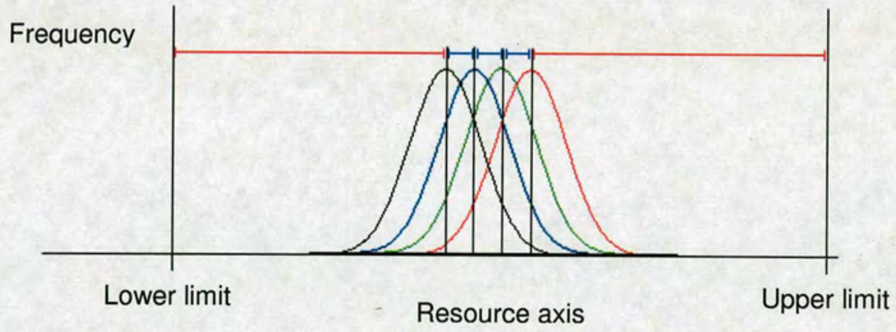


Figure 1.2 Two different species distributions between dawn and dusk. Each curve represents variation within a single species around a species mean. The blue lines show the distances between species used to calculate Williams' *V* statistic when the range is taken between the first and last peak, and the red lines show additional distances that will be included in the calculation of the statistic if the range is between dawn and dusk.

## 1.5 Temporal structure in community-level plant-pollinator interactions

To date, studies of plant-pollinator interactions in daily time have considered only closely related plant species. However, most plant-pollinator interactions will be embedded within a highly complex web of interactions involving multiple plant and pollinator species. The majority of plant and pollinator species are generalists and interact with multiple partners (Waser et al. 1996, Waser and Ollerton 2006). Therefore, we might expect competition for pollinators to exist among plant species at a community level, and that plant species might diverge along one of the resource axes listed in Section 1.1 to reduce competition. In addition, plants might interact to facilitate each other's reproduction at a community level.

Acacias are a subset of an entire flowering plant community and thus have the potential to interact via pollinators with other flowering plant species. Therefore consideration of acacias as a group that interact solely with one another may be an oversimplification. Most acacias produce little or no nectar, and bees that forage on acacias for pollen must often visit other floral resources to obtain nectar. Inclusion of other plants as potential interactors with acacias reflects the growing realisation that most communities are best studied as interaction webs. This has long been applied to food webs, and in Chapter 6 I describe the development of web-based approaches to plant-pollinator interactions. This is the first study to adopt an interaction web-based perspective of daily temporal structure.

Both 'top down' and 'bottom up' factors can influence daily temporal structure in plant-pollinator interactions. Firstly, the timing of pollinator visits might be restricted by daily nesting cycles (e.g. bees) or because of thermoregulatory requirements (Willmer and Stone 2004). Secondly, plants might release pollen and/or nectar at particular times of day which will influence the visitation patterns of pollinators.

In this thesis I examine flowering plant communities at different seasonal times for temporal structure in plant-visitor interactions over daily timescales. This approach requires qualifying visitation by all flower visitors for all flowering plant species in a community. I use a newly developed null modelling approach to assess evidence for daily temporal structure among plant-visitor interactions.

## 1.6 Thesis outline

In this thesis I examine a multi-species acacia assemblage and entire flowering plant communities in a Kenyan savannah habitat for evidence of structure in plant-pollinator interactions over seasonal and daily timescales.

In Chapter 2, I discuss the study species and describe the study location for all work in this thesis.

In Chapter 3, I ask whether the acacias at the study location regularly co-flower and which species most often co-flower.

In Chapter 4, I ask at what time the acacias dehisce during the day, and whether species that commonly co-flower show daily structure in pollen release compatible with competitive displacement. Specifically I assess the evidence for intraspecific synchrony and interspecific dispersion.

In Chapter 5, I look in detail at the visitor assemblages of the acacias and ask (i) whether shared pollinators make significant proportions of visits and (ii) if the daily activity sequence of shared pollinators matches the sequence of dehiscence across co-flowering species.

In Chapter 6, I ask whether acacias share visitors with other plant species and whether daily temporal structure exists among plant-visitor interactions at a community scale.

In Chapter 7, I summarise the findings of this thesis, discuss the implications of this work and describe possible future studies.

# Chapter 2. Study sites and species

In this chapter I describe the study location and then discuss the study species, including the current taxonomic status of the genus *Acacia*. Finally I describe the sampling sites at which fieldwork was conducted.

## 2.1 Study location: Mpala Research Centre

All fieldwork for this project was conducted in semi-arid savannah habitat at Mpala Research Centre (37°52'E, 0°17'N), located in Laikipia District, Central Kenya (Fig. 2.1). Mpala Research Centre is part of the Mpala Wildlife Conservancy, a 20,000 hectare (48,000 acre) property bordered on the east side by the Ewaso Ng'iro river, and to the north by the Ewaso Narok river. The Mpala property is situated northwest of Mt. Kenya and Nanyuki town, 50km north of the Equator.

Mpala is managed for cattle production using traditional Maasai herding methods (Augustine et al. 2003). Herders construct temporary accommodation, enclosed by bomas (fences of cut thorny vegetation) to protect the livestock at night. These bomas are relocated periodically depending on food and water availability. No local communities are resident on the property. Human habitation is limited to two main areas with research buildings and accommodation in the south and a ranch house in the east. A dirt road running from north to south is one of the main access roads for the region. The boundaries are unfenced, allowing wildlife to move freely across the property.

### 2.1.1 Climate

The climate is semi-arid, with warm days and cool nights. Climate varies across the property with altitude; the southwest is higher (1850m a.s.l.), wetter and cooler, and the northeast is lower (1550m a.s.l.), drier and hotter (Mpala Wildlife Foundation 2006). Humidity is lowest in the dry season (January-March) and in September, which is also a relatively dry month (Paton 2004). Mean daily relative humidity between 1999 and 2003 was 62.5% (Paton 2004). Rainfall follows a weakly trimodal pattern (Fig. 2.2) with long rains in April-May and shorter periods of rain in July-August and October-November (Mpala Wildlife Foundation 2006).

Monthly rainfall data collected by Mpala Research Centre at the location of the research centre buildings between May 1998 and December 2005 are shown in Table 2.2 and mean monthly totals are shown in Figure 2.2. Mean annual rainfall between 1999 and 2005 was 617 mm (Table 2.1). Rainfall is unpredictable and can vary considerably between years; total annual rainfall between 1999 and 2005 varied between 350mm (2000) and 837mm (2001) (Table 2.1).

Figure 2.1 A map of Kenya and neighbouring countries showing the locations of acacia pollination studies in East Africa: **Mpala** the study location for this thesis, **Kositei**, the location of *Vachellia nilotica* studies conducted by Tybirk (1988, 1989, 1993) and **Mkomazi**, the study location in Tanzania for Stone et al. (1996, 1998, 1999a). (Source: Mountain High Maps. Adapted by G. N. Stone)

Table 2.1 Monthly rainfall totals at Mpala Research Centre, May 1998-December 2005. Data were collected by Mpala Research Centre.

| | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | Mean |
|---|---|---|---|---|---|---|---|---|---|
| Jan | | 8.6 | 0.8 | 46.9 | 8.9 | 0.0 | 90.3 | 17.2 | 24.7 |
| Feb | | 0.0 | 0.0 | 0.0 | 0.0 | 12.0 | 19.4 | 23.8 | 7.9 |
| March | | 73.9 | 0.0 | 55.7 | 43.3 | 12.2 | 48.8 | 18.2 | 36.0 |
| April | | 18.1 | 4.8 | 188.0 | 110.2 | 245.1 | 207.9 | 115.5 | 127.1 |
| May | 42.3 | 34.3 | 31.4 | 48.8 | 70.8 | 82.9 | 65.7 | 128.4 | 63.1 |
| June | 49.1 | 2.2 | 22.7 | 70.8 | 21.0 | 36.2 | 2.4 | 24.6 | 28.6 |
| July | 68.3 | 100.3 | 61.0 | 48.3 | 33.0 | 38.8 | 89.4 | 21.2 | 57.5 |
| Aug | 106.4 | 59.5 | 153.9 | 54.7 | 3.7 | 123.7 | 80.3 | 49.5 | 79.0 |
| Sep | 35.3 | 17.7 | 7.5 | 8.5 | 9.2 | 30.0 | 68.5 | 102.5 | 34.9 |
| Oct | 76.1 | 19.5 | 20.2 | 52.9 | 59.5 | 13.2 | 37.2 | 30.6 | 38.7 |
| Nov | 107.0 | 57.0 | 30.9 | 231.1 | 82.5 | 113.2 | 118.3 | 20.8 | 95.1 |
| Dec | 2.6 | 19.7 | 16.6 | 11.0 | 91.1 | 46.0 | 8.8 | 0.0 | 24.5 |
| **Total** | **487.1** | **410.8** | **349.8** | **816.7** | **533.2** | **753.3** | **837.0** | **552.3** | **617.0** |

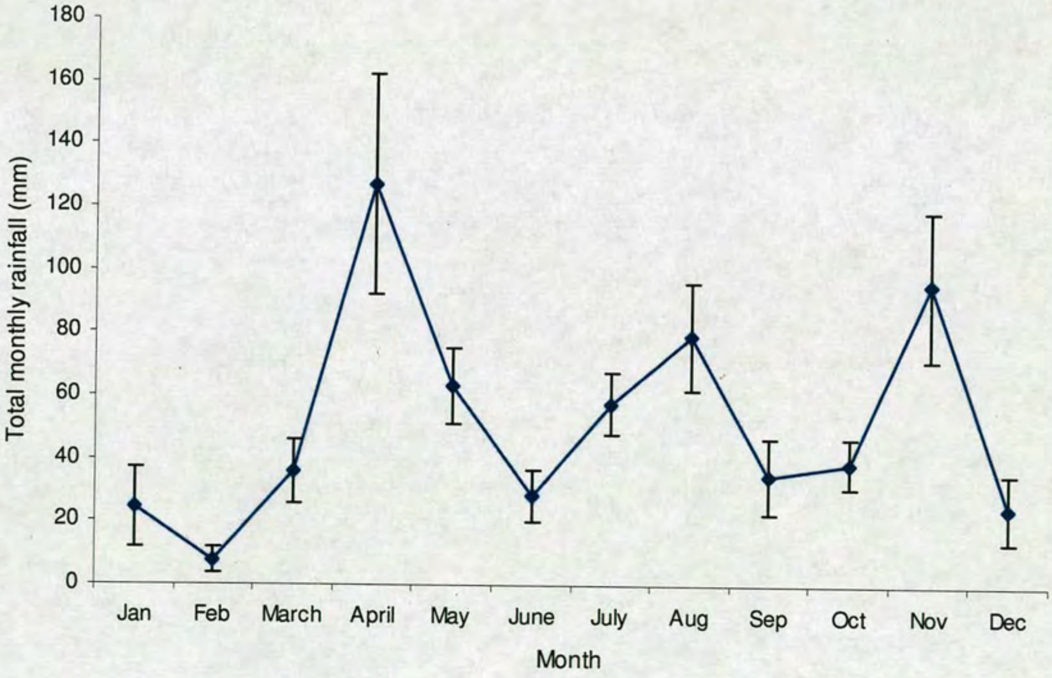


Figure 2.2 Mean monthly total rainfall at Mpala Research Centre between May 1998 and December 2005 (± 1SE). Full data are shown for all years individually in Appendix 3. Data were collected by Mpala Research Centre.

## 2.1.2 Geology and soil types

There are three types of soil on the Mpala property (Fig. 2.3). A higher plateau of black cotton soil, a deep clay vertisol with impeded drainage that is seasonally inundated is found in the south west of the property. As the plateau descends in the south east and north of the property, this gives way to well drained thin red sandy loams (latosols) at lower elevations. Intermediate soil is known as 'transition soil'. Granitic inselbergs, or kopjes, are scattered throughout the terrain.

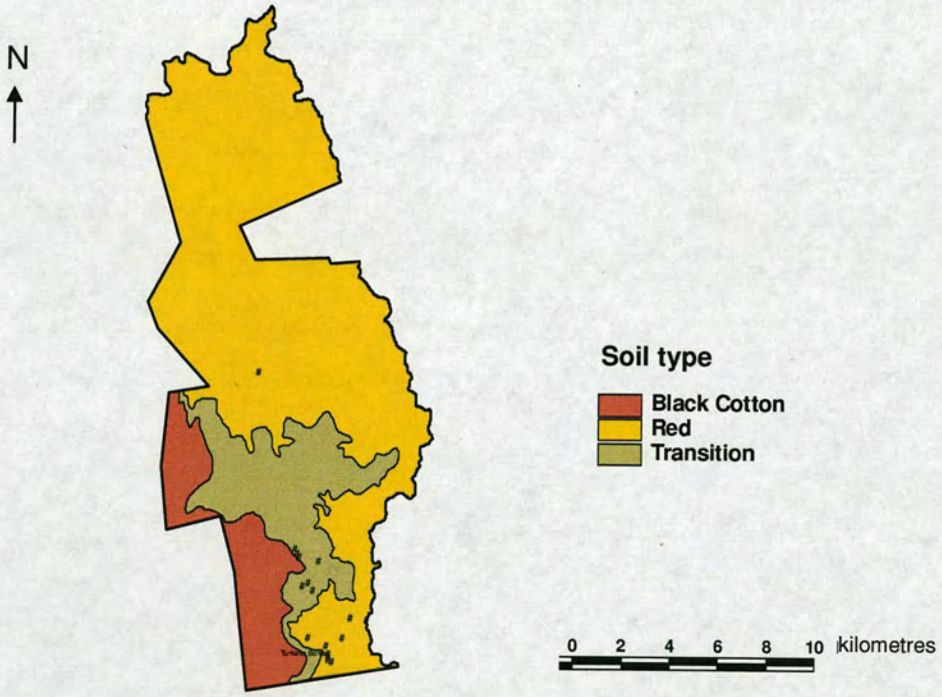


Figure 2.3 Distribution of soil types at Mpala. Points marked are sampling sites that will be described in more detail in section 2.3.1. This map was drawn using GIS information provided by Mpala Research Centre.

## 2.2 Study species

Chapters 3 to 5 examine the pollination ecology of ten species that until recently were part of the genus *Acacia* Miller (Fabaceae: Mimosoideae). However, recent phylogenetic analyses have shown that the genus is polyphyletic (Miller and Bayer 2001, 2003, Maslin et al. 2003) and it has subsequently been split into five genera. I will start this section with a brief taxonomic history of the genus *Acacia*, before discussing the five genera that now exist and then move on to describing the study species at Mpala.

### 2.2.1 Taxonomy of the genus *Acacia*

The genus *Acacia* was first described by Philip Miller in 1754 and revised by George Bentham in 1842 who restricted the name *Acacia* to mimosoid plants having numerous free stamens (Maslin et al. 2003). Bentham also defined the tribes of the subfamily Mimosoideae. The tribe Acacieae incorporated all *Acacia* species along with the genus *Faidherbia*, whilst taxa with fused stamens were assigned to the tribe Ingaeae. In 1972 Jacques Vassal described three subgenera within *Acacia*, based on his own studies of seeds, seedlings and stipules, and palynological studies by Guinet (1969): *Acacia*, *Aculeiferum* and *Heterophyllum* (=*Phyllodineae*). Pedley (1986) was the first author to propose the division of *Acacia* into three separate genera, namely *Acacia*, *Senegalia* Rafinesque and *Racosperma* C.Martius., corresponding to subgenus *Acacia*, subgenus *Aculeiferum* and subgenus *Phyllodineae* respectively. This proposal was not widely adopted, however it was recognised at the time that differences did exist within *Acacia* and that more comprehensive information was needed to make informed decisions regarding the status of the genus (Maslin 1988).

A number of morphological and molecular studies have been undertaken in recent years to assess the taxonomic and phylogenetic status of *Acacia* and tribe Acacieae (reviewed in Maslin et al. 2003). These studies suggested that five taxonomic groups exist within *Acacia* and, whilst confirming that subgenus *Acacia* and subgenus *Phyllodineae* were monophyletic, found that subgenus *Aculeiferum* was formed of three monophyletic assemblages (Maslin et al. 2003). These three groups were termed subgenus *Aculeiferum* sensu stricto, subgenus *Aculeiferum* section *Filicinae* and the '*Acacia coulteri*' group (Maslin et al. 2003). On the basis of these studies it was widely accepted that the generic status of species within the genus *Acacia* needed to be revised and new generic names have been assigned to each of the five groups (see Table 2.2). Retypification of the type specimen of *Acacia* from the African species *Acacia scorpioides* (L.) W. Wight (=*A. nilotica*) to the Australian species *A. pennivervis* Sieber ex DC, as proposed by Orchard and Maslin (2003), was endorsed at the Nomenclature Session of the 17th International Botanical Congress (IBC) in Vienna in July 2005 (Smith et al. 2006). This means that all species in the subgenus *Phyllodineae*, which includes the majority of the Australian species, will retain the generic name *Acacia*, whereas species belonging to the subgenus *Acacia* will be assigned the genus name *Vachellia* Wight & Arnott, the earliest known alternative name. The three monophyletic groups forming the genus *Aculeiferum* have been assigned the names *Senegalia* Rafinesque (subgenus *Aculeiferum* sens. str.), *Acaciella* Britton & Rose (subgenus *Aculeiferum* sect. *Filicinae*) and *Mariosousa* Seigler and Ebinger (*A. coulteri* group) (Seigler et al. 2006b).

New combinations have been made for some American species of *Vachellia* and *Senegalia* (Seigler and Ebinger 2005, Seigler et al. 2006a) although as yet the new names have not been widely adopted. Since it is likely that new combinations will be made for species in the former subgenera *Acacia* and *Aculeiferum* in the near future, in this thesis all species are named using the new classification system. I shall use the term 'acacia' to encompass all species previously and currently belonging to the genus *Acacia*.

Table 2.2 Main classifications of *Acacia* from Vassal (1972) through to the current five genera into which *Acacia* has now been divided.

| Subgenera proposed by Vassal (1972) | Adopted subgenera | Genera proposed by Pedley (1986) | Taxonomic groups within *Acacia* (Maslin et al. 2003) | New generic names |
|---|---|---|---|---|
| *Acacia* | *Acacia* | *Acacia* | subg. *Acacia* | *Vachellia* |
| *Aculeiferum* | *Aculeiferum* | *Senegalia* | subg. *Aculeiferum* sensu stricto | *Senegalia* |
| *Aculeiferum* | *Aculeiferum* | *Senegalia* | subg. *Aculeiferum* sect. Filicinae | *Acaciella* |
| *Aculeiferum* | *Aculeiferum* | *Senegalia* | '*Acacia coulteri*' group | *Mariosousa* |
| *Heterophyllum* | *Phyllodineae* | *Racosperma* | subg. *Phyllodineae* | *Acacia* |

### 2.2.2 Genera formerly belonging to *Acacia*

Species belonging to the five genera into which the genus *Acacia* has now been subdivided are dominant woody trees and shrubs found throughout the world in tropical, subtropical and warm temperate regions. Most species occur in regions where the rainfall is markedly seasonal or low (Ross 1981). The distribution of the five genera varies worldwide and is described, along with the morphological characteristics for each genus, in Maslin et al. (2003). Seigler et al. (2006b) describe the morphological characters that distinguish *Senegalia* from *Acaciella* and *Mariosousa*.

Table 2.3. Numbers of accepted, described species of acacias now belonging to the genera *Vachellia*, *Senegalia*, *Acaciella*, *Mariosousa* and *Acacia* (following Maslin et al. 2003 and adapted from www.worldwidewattle.com)

| Revised generic name | Americas | Africa[1] | Asia | Australia & Pacific | Total species |
|---|---|---|---|---|---|
| *Vachellia* | c. 60 | 73 | 36[2] | 9 | c. 163 |
| *Senegalia* | 97 | 69 | 43[3] | 2[4] | 203 |
| *Acaciella* | 15 | - | - | - | 15 |
| *Mariosousa* | 13 | - | - | - | 13 |
| *Acacia* | - | 2[5] | 10 | 982[6] | 987 |
| Total species | c. 185 | 144 | 89 | 993 | 1381 |

[1] Includes Madagascar, Reunion and Mauritius;
[2] Including c. 15 species also found in Africa;
[3] Including 7 species also found in Africa;
[4] Including 1 species also found in Asia;
[5] 2 species in Madagascar, Reunion and Mauritius;
[6] 975 species in Australia, 7 species in the Pacific.

*(a) Vachellia*

Species of *Vachellia* (previously *Acacia* subgenus *Acacia*) are distributed throughout Africa (including Madagascar) (73 species), Asia (36 species, including c. 15 species that also occur in Africa) and the Americas (c. 60 species) (Table 2.3, Fig. 2.4a). A small number of species are found in the northern tropical regions of Australia. *Vachellia* are trees or shrubs with bipinnate leaves, paired stipular spines and no prickles (Maslin et al. 2003).

*(b) Senegalia*

*Senegalia* species are distributed throughout Africa (69 species), Asia (43 species, including c. 7 species that also occur in Africa) and the Americas (97 species), with two species found in northern Australia (Table 2.3, Fig. 2.4b). *Senegalia* are trees or shrubs with bipinnate leaves that have no stipular spines, but usually have two or three straight or recurved prickles near the stipules (Maslin et al. 2003).

### *(c) Mariosousa*

The recently proposed genus *Mariosousa* consists of 13 species (Seigler et al. 2006b). The distribution is restricted to tropical and subtropical regions of the southwestern United States, Mexico and Central America (Table 2.3, Fig. 2.4c). *Mariosousa* species have bipinnate leaves and are morphologically distinct from *Senegalia* and *Acaciella* species in that they always lack prickles and are never lianas.

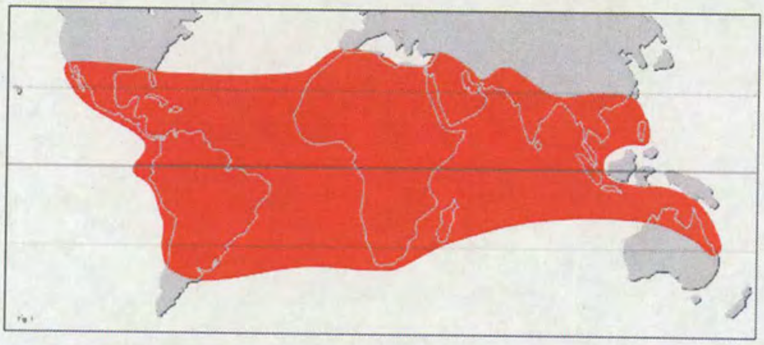
### *(d) Acaciella*

This proposed genus consists of 15 species and is only found in the Americas (Table 2.3, Fig. 2.4d). The distribution of *Acaciella* extends from the south-central United States to Argentina, with the highest concentration of species occurring in Mexico (Maslin et al. 2003). Species are trees or shrubs and have bipinnate leaves and no prickles or stipular spines.

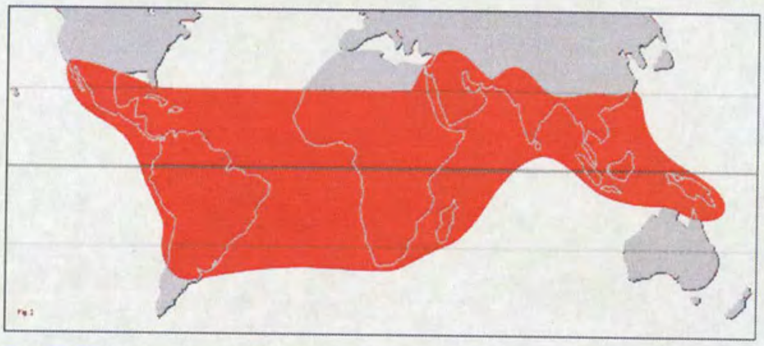
### *(e) Acacia*

The predominantly Australian genus *Acacia* (previously subgenus *Phyllodineae*) contains 987 described species and is the most diverse acacia genus. Most species are found in Australia, although a small number are found in the Pacific region east to Hawaii, in Asia north to Taiwan and in Madagascar, Reunion and Mauritius (Table 2.3, Fig. 2.4e). Species are trees or shrubs that sometimes have stipular spines but never have prickles. Most species have leaves reduced to a flattened rachis, known as a phyllode.

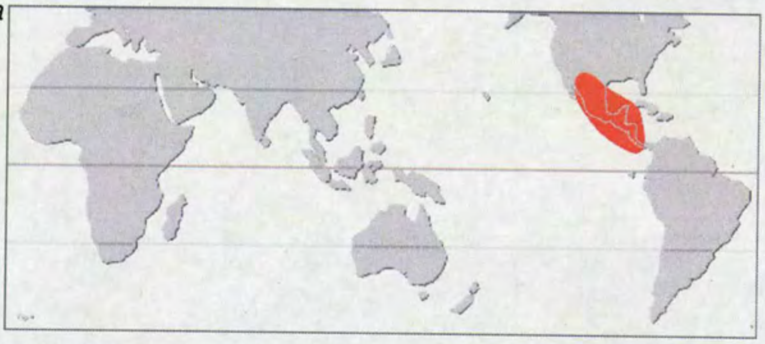
(a) *Vachellia*



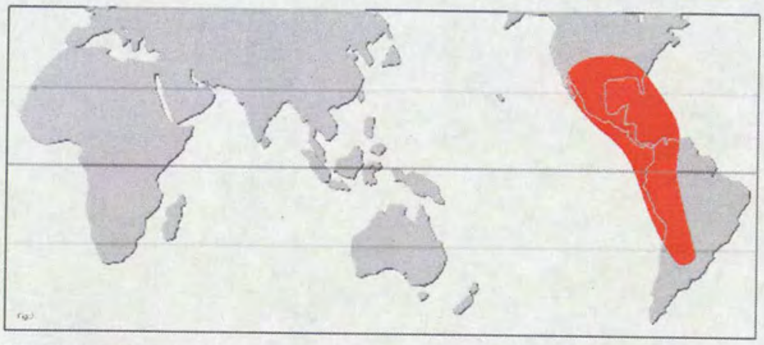
(b) *Senegalia*



(c) *Mariosousa*



(d) *Acaciella*



(e) *Acacia*

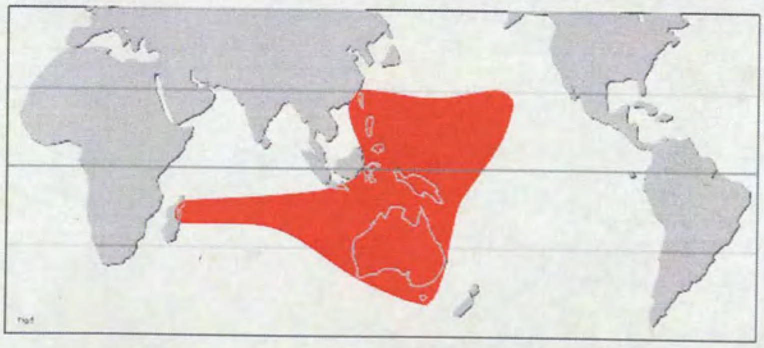


Figure 2.4 Distributions of the five acacia genera: (a) *Vachellia*, (b) *Senegalia*, (c) *Mariosousa*, (d) *Acaciella* and (e) *Acacia*. Distribution maps are freely available from www.worldwidewattle.com

### 2.2.3 Phylogenetic relationships within the Mimosoideae

Molecular and morphological studies have also revealed further information regarding the relationships between the five acacia genera and other tribes and genera in the subfamily Mimosoideae, although some of these studies give conflicting results and the exact phylogenetic relationships remain unclear (reviewed in Maslin et al. 2003). Figure 2.5 shows a schematic tree based on studies of chloroplast DNA sequence data by Miller and Bayer (2000, 2001, 2003) and Luckow et al. (2003), which suggests that the taxa in the tribe Acacieae (genera *Acacia*, *Vachellia*, *Senegalia*, *Mariosousa*, *Acaciella* and *Faidherbia*) may not be distinct from those in the tribes Ingaeae and Mimoseae, with *Vachellia* more closely related to basal mimosoid tribes and the other genera more closely related to the tribe Ingaeae. Kergoat et al. (2007) found results consistent with this in the examination of the beetle seed predators associated with acacias and related taxa.

Maslin et al. (2003) advised caution in interpreting the results of the earlier studies and recommend that further work should incorporate further data from basal taxa in the subfamily, as well as from closely related taxa in the subfamily Caesalpinioideae.

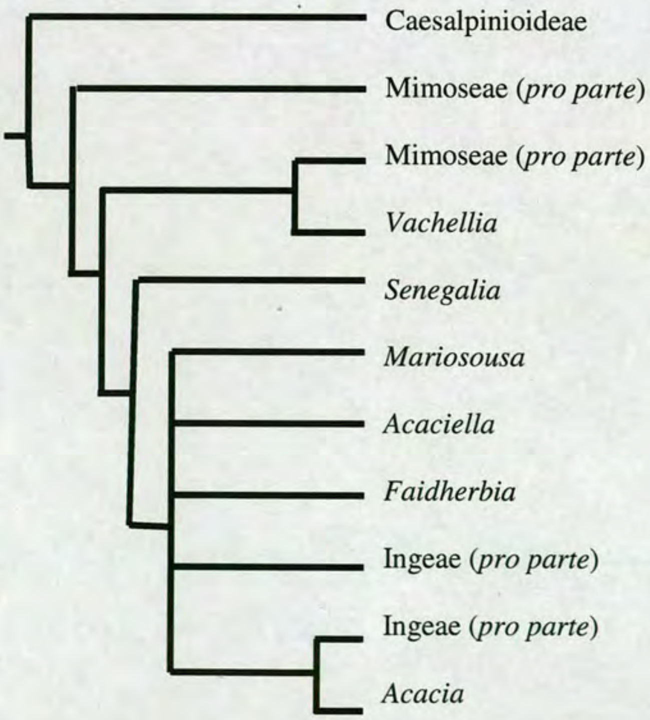


Figure 2.5 A schematic diagram showing the relationships between taxa in the subfamily Mimosoideae based on studies of chloroplast DNA sequence data by Miller and Bayer (2000, 2001, 2003) and Luckow *et al.* (2003) (adapted from Maslin et al. 2003).

### 2.2.4 Acacia species at Mpala

African acacias in the genera *Vachellia* (previously *Acacia* subgenus *Acacia*) and *Senegalia* (previously part of *Acacia* subgenus *Aculeiferum*) are thorny trees and bushes that dominate the woody vegetation in savannah habitats (Coe and Beentje 1991). Acacias are key species in these habitats, providing food and other resources for a large diversity of mammals, birds and invertebrates (e.g. Kruger and McGavin 1998, Bond and Loffell 2001, Dean et al. 2002). Of the 142 acacia species found in mainland Africa (excluding species found solely in Madagascar) 73 belong to the genus *Vachellia* and 69 to the genus *Senegalia* (www.worldwidewattle.com). The East African region contains the highest acacia species diversity on the continent and Kenya has the second highest diversity of any country after Tanzania, with 27 and 15 species in the genera *Vachellia* and *Senegalia* respectively (Ross 1981).

Ten acacia species are found at Mpala: *Senegalia brevispica*, *Senegalia mellifera*, *Vachellia drepanolobium*, *Vachellia etbaica*, *Vachellia gerrardii*, *Vachellia hockii*, *Vachellia nilotica*, *Vachellia seyal*, *Vachellia tortilis* and *Vachellia xanthophloea*. *Vachellia seyal* is present in two forms: *V. seyal* var. *seyal* and *V. seyal* var. *fistula*. These are listed along with the old generic and subgeneric names and the authorities for these in Table 2.4. Some examples of these species are shown in Figures 2.7 and 2.8.

Table 2.4 Names for the Mpala acacia species under the new classification of acacia genera, along with their old species names, subgenera and authorities.

| New name | Old name | Old subgenus | Authority for old name |
|---|---|---|---|
| *Senegalia brevispica* | *Acacia brevispica* | *Aculeiferum* | Harms. |
| *Senegalia mellifera* | *Acacia mellifera* | *Aculeiferum* | (Vahl) Benth. |
| *Vachellia drepanolobium* | *Acacia drepanolobium* | *Acacia* | Sjöstedt |
| *Vachellia etbaica* | *Acacia etbaica* | *Acacia* | Schweinf. |
| *Vachellia gerrardii* | *Acacia gerrardii* | *Acacia* | Benth. |
| *Vachellia hockii* | *Acacia hockii* | *Acacia* | De Wild. |
| *Vachellia nilotica* | *Acacia nilotica* | *Acacia* | (L.) Del. |
| *Vachellia seyal* | *Acacia seyal* | *Acacia* | Del. |
| *Vachellia tortilis* | *Acacia tortilis* | *Acacia* | (Forssk.) Hayne |
| *Vachellia xanthophloea* | *Acacia xanthophloea* | *Acacia* | (S.Moore) Taub. |

Species composition varies between soil types (Table 2.5). The red soil vegetation is mainly composed of *Senegalia brevispica* and *Vachellia etbaica* along with *Senegalia mellifera*, *Vachellia gerrardii* and *Vachellia nilotica* (Young et al. 1995). *Vachellia drepanolobium* (whistling thorn acacia) is found in low densities on the red soil but is the dominant woody plant species on the black cotton soil, accounting for more than 98% of the overstory vegetation (Young et al. 1998). *Vachellia xanthophloea* (yellow fever tree), grows in close proximity to water and is found along river banks and near some of the man-made dams on the property. Three other species, *Vachellia seyal*, *Vachellia hockii* and *Vachellia tortilis*, are comparatively rare and have limited distributions at Mpala. The Mpala habitat is shown in Figure 2.10.

### 2.2.5 The plant community at Mpala

The vegetation at Mpala is characteristic of semi-arid African savannahs. Grassy woodland predominates and is interspersed with patches of woodland and open grassland (Mpala Wildlife Foundation 2006). The woody vegetation is dominated by acacias in the genera *Senegalia* and *Vachellia* but also includes *Croton dichogamus* (Euphorbiaceae) as well as shrubs in the genera *Grewia* (Tiliaceae), *Rhus* (Anacardiaceae), *Balanites* (Balanitaceae) and *Boscia* (Capparaceae) (Young et al. 1995, Mpala Wildlife Foundation 2006).

In addition to differing compositions of acacia species, the understory layers of the two soil types are also characteristically different. The red soil is dominated by perennial grasses including *Cynodon dactylon*, *Digitaria milanjiana*, *Pennisetum mezianum* and *P. stramineum* (Augustine et al. 2003, Augustine 2003) with the herbs *Plectranthus* spp., *Portulaca* spp., *Pollichia campestris* and *Blepharis* spp. (Young et al. 1995). The understory of the black cotton soil vegetation is dominated by the grasses *Themeda triandra*, *Pennisetum stramineum*, *P. mezianum*, *Lintonia nutans* and *Brachiaria lachnatha* and the herbs *Aerva lanata*, *Rhinacanthus ndorensis*, *Dyschoriste radicans*, and *Commelina* spp. (Young et al. 1997).

There are 516 recorded plant species at Mpala, with 385 species of dicotyledonous plants in 60 families and 113 species of monocotyledons in 17 families (Young 2000). However this list is not comprehensive and many more plant species could be present. In Chapter 6 of this thesis I consider plant-pollinator interactions at the level of entire flowering plant communities at two sites at Mpala.

Plant species were identified with the aid of Blundell (1992) and keys in Agnew and Agnew (1994). Much of the identification to species level was carried out by Professor Andrew Schnabel (Indiana University South Bend), a long term collaborator with the project. Full details of non-acacia plant species studied are provided in Chapter 6 and associated appendices. Some examples of the flowering plant species at Mpala are shown in Figures 2.11 and 2.12.

Table 2.5 Distribution of the acacia species at Mpala, growth form, flower shape and colour, and the presence of floral nectar

| Species | Distribution | | Growth form (from Coe and Beentje 1991) | Flower shape | Flower colour | Floral nectar |
|---|---|---|---|---|---|---|
| | red soil | black cotton soil | | | | |
| *Senegalia brevispica* | widespread | rare | Small tree or shrub to 7m or scandent shrub to 12m | spherical | white | trace |
| *Vachellia drepanolobium* | widespread | dominant | Shrub or tree 1-7.5m. Either short and robust, or a slender tree with rounded canopy | spherical | white | not known |
| *Vachellia etbaica* | widespread | rare | Tree, from 2-12m | spherical | white | not known |
| *Vachellia gerrardii* | widespread | not found | Flat topped or spindly tree to 15m | spherical | white | not known |
| *Vachellia hockii* | rare | not found | Shrub or tree to 6m, may reach 9m, with flattened crown | spherical | yellow | not known |
| *Senegalia mellifera* | widespread | rare | Dense obconical or small tree, to 9m | elongate | white | nectar |
| *Vachellia nilotica* | widespread | not found | Flat or rounded crown, to 12m | spherical | yellow | no nectar |
| *Vachellia seyal var. seyal* | rare | not found | Tree with flattened spreading crown, to 12m | spherical | yellow | not known |
| *Vachellia seyal var. fistula* | rare | rare | | spherical | yellow | not known |
| *Vachellia tortilis* | rare in south, common in north | not found | Tree to 18m, flattened crown, sometimes restricted to a small shrub | spherical | white | not known |
| *Vachellia xanthophloea* | common on river banks | not found | Tall tree, up to 25m | spherical | white | not known |

### 2.2.6 The floral biology of *Vachellia* and *Senegalia* species

All acacias present their flowers in the form of a compound flower head. The morphology of flower heads differs between *Vachellia* and *Senegalia*. *Vachellia* species generally have spherical (globose) flower heads whereas *Senegalia* species commonly bear elongate (spicate) flower heads. Not all species conform to this pattern. For example, *Senegalia brevispica* has spherical flower heads. Almost all species have flower heads that are white, cream or yellow, with *Senegalia* flower heads either white or cream, and *Vachellia* flower heads ranging from white through to bright yellow (Coe and Beentje 1991, Fig. 2.9). Details of flower head structure and colour for the Mpala acacias are given in Table 2.5.

Acacias produce two types of floral rewards for pollinators; pollen and nectar. Pollen is presented on the surface of flower heads in the form of compound pollen grains, termed polyads (Kenrick and Knox 1982, 1989, Kenrick 2003). Each stamen bears an anther containing eight polyads, with each polyad containing 4, 8, 16 or 32 pollen grains, depending on the species (Kenrick and Knox 1989, Kenrick 2003). The number of stamens per flower and the number of flowers per flower head vary substantially between species, but also within species (Tybirk 1989, 1993, Sedgley et al. 1992, Kenrick 2003, Stone et al. 2003). In some acacia species all flowers are hermaphrodite, with a central stigma surrounded by stamens, whilst in others a proportion of flower heads on an individual tree are purely male and contain only stamens (Tybirk 1989, Sedgeley et al. 1992, Kenrick 2003, Stone et al. 2003). As well as contributing to reproduction through male function, these flowers may be important in recruiting a limited pool of pollinators through provision of an abundant reward.

Some species of *Vachellia* and *Senegalia* also produce floral nectar. Nectar secretion is known for some African acacias in each genus (Stone et al. 1998, Tandon et al. 2001, Stone et al. 2003). Nectar quality and quantity varies among species (Stone et al. 2003). In comparison Australian acacias in the genus *Acacia* produce no nectar, although several species have extra-floral nectaries that attract a wider diversity of floral visitors (Bernhardt 1987, Kenrick 2003).

The flowers of both genera are typically protandrous and last for a single day (Tybirk, 1989, 1993, Stone et al. 1996, Willmer and Stone 1997a). Flowers on an individual head commonly open synchronously in *Vachellia*, but can open in groups over 2-3 days in some *Senegalia* species (Stone et al. 2003). The reproductive biology of acacias is reviewed in detail by Kenrick (2003).

## 2.3 Sampling sites

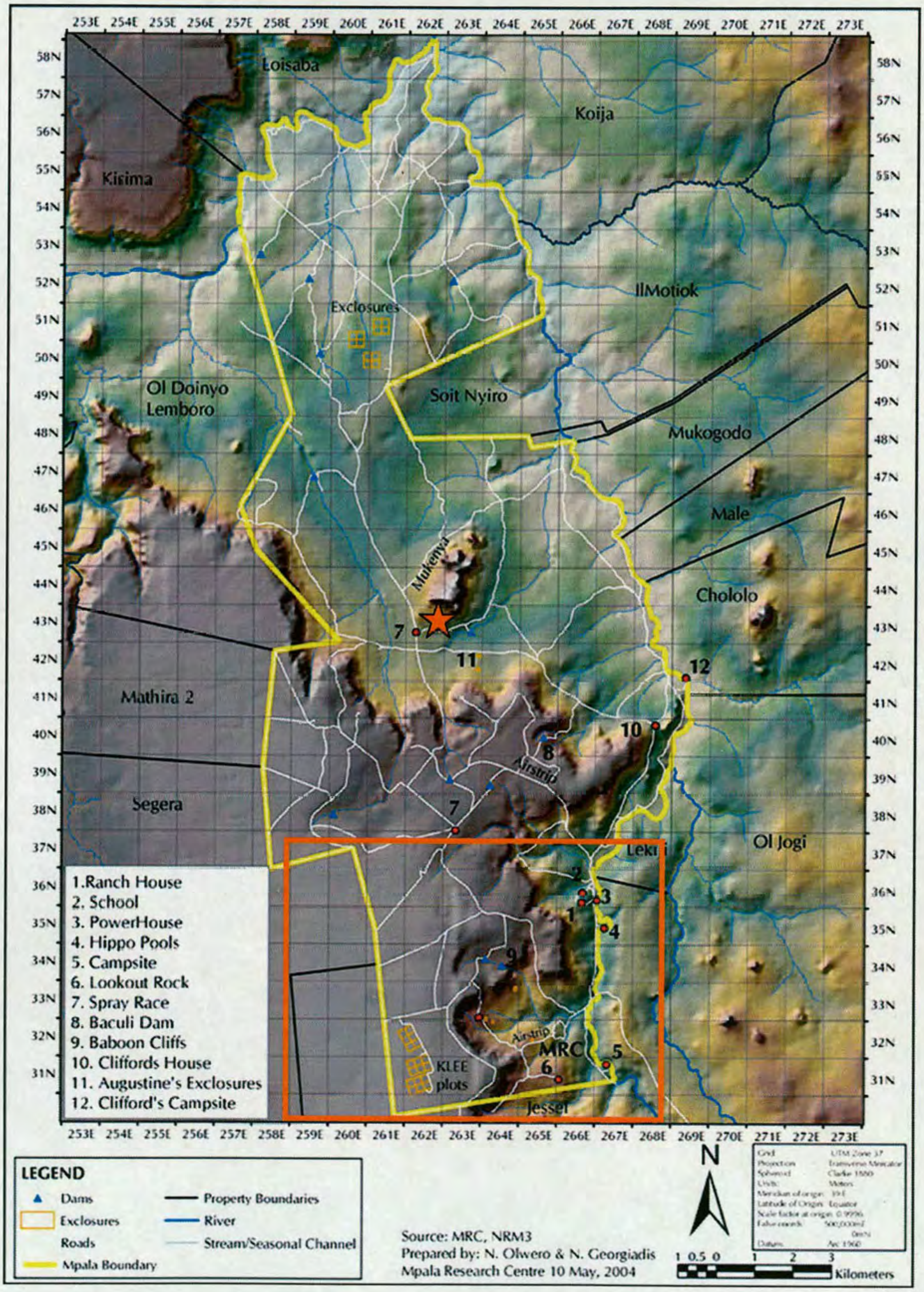
Data collection for this thesis took place at eight sampling sites at Mpala. These sites were established in 1998 and 1999 for the collection of long term data on the flowering and fruiting patterns of acacia species. Seven of these sites are located in the south of the property within 7 km of the main centre buildings (Figs. 2.5, 2.6). The eighth site, Mukenya, is located in the north of the property, approximately 15 km north of the centre buildings (Fig. 2.5).

Most sites were located on red soil (Table 2.6). Junction and High Dam were located on transition soil. Although the diversity of acacia species was similar (Table 2.6), the vegetation and topology differs between the red soil and transition soil sites. The vegetation at transition soil sites was less dense with acacia trees more widely dispersed than at red soil sites. The understory shrub layers also contained different species (see Appendix 7 for a comparison of flowering plant species recorded on both soil types in June and July 2004). There were topological differences between the red and transition soil sites; the terrain at Junction and High Dam was rockier and the sites were located near the top of an escarpment that rises from the south of the property towards a plateau and then descends in the north.

At each site marked acacia trees were monitored twice a month for flower head and fruit abundance. Some of these data are examined in Chapter 3. Patterns of pollen availability and visitation to flower heads were examined for acacia trees at MRC (Mpala Research Centre buildings), Turkana Boma, Mongoose, High Dam and Junction (Chapters 4 and 5). Permanent marked plots were established at Turkana Boma and Junction for the collection of community-level flower-visitor interaction data (Chapter 6). These sites were chosen to encompass the diversity of soil types and vegetation at Mpala.

Table 2.6. Sampling sites, height a.s.l., soil type, year established and acacia species composition. Species with asterices were not sampled at that site in the phenology study (Chapter 3).

| Site name | Height m. a.s.l. | Year site established | Soil type | Acacia species |
|---|---|---|---|---|
| MRC | 1716 | 1998 | red | *S. brevispica*<br>*V. etbaica*<br>*V. nilotica*<br>*S. mellifera* |
| Turkana Boma | 1732 | 1998 | red | *S. brevispica*<br>*V. drepanolobium*<br>*V. etbaica*<br>*V. gerrardii*<br>*V. nilotica*<br>*V. seyal* var. *seyal*<br>*S. mellifera* |
| Mongoose | 1718 | 1998 | red | *V. brevispica*<br>*V. drepanolobium*<br>*V. gerrardii*<br>*V. mellifera* |
| Mukenya | 1696 | 1998 | red | *S. brevispica*<br>*V. etbaica*<br>*S. mellifera*<br>*V. nilotica* |
| Junction | 1801 | 1998 | transition | *S. brevispica*<br>*V. drepanolobium*<br>*V. etbaica*<br>*V. gerrardii*<br>*V. hockii*<br>*V. nilotica*<br>*V. seyal* var. *seyal*<br>*S. mellifera* |
| High Dam | 1776 | 1999 | transition | *S. brevispica*<br>*V. gerrardii*<br>*V. hockii*<br>*V. nilotica*<br>*S. mellifera* |
| Boma | 1690 | 1999 | red | *V. tortilis*<br>*V. brevispica* *<br>*V. etbaica* *<br>*S. mellifera* *<br>*V. nilotica* * |
| River | 1660 | 1999 | red | *V. xanthophloea* *<br>*S. brevispica* *<br>*V. etbaica* *<br>*V. nilotica* * |



Source: MRC, NRM3
Prepared by: N. Olwero & N. Georgiadis
Mpala Research Centre 10 May, 2004

Figure 2.5 A map of the Mpala property. Darker areas in the southwest of the property represent the black cotton soil plateau. The Mukenya sampling site is marked with a star. The other sites are found within the marked area in the southern part of the property and specific locations are shown in the larger scale map in Fig. 2.6 This map was prepared by N. Olwero and N. Georgiadis.

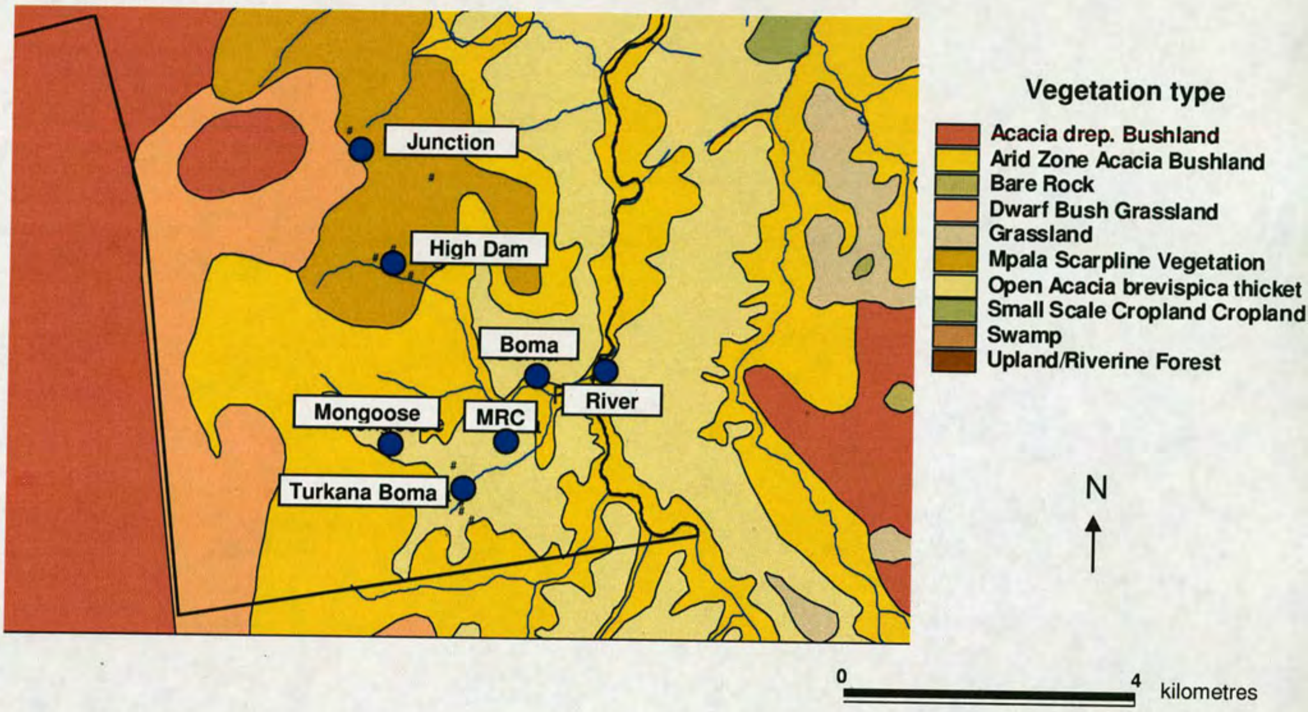


Figure 2.6 Sampling site locations at Mpala. Each site is marked by a blue dot. This map was drawn using GIS information provided by Mpala Research Centre.

(a) *Senegalia mellifera*

(b) *Vachellia hockii*

(c) *Vachellia tortilis*

(d) *Senegalia brevispica*

(e) *Vachellia xanthophloea*

Figure 2.7 Acacia species found at Mpala

(a) *Vachellia gerrardii*

(b) *Vachellia nilotica*

(c) *Vachellia drepanolobium* in flower

Figure 2.8 Acacia species found at Mpala

(a) *Senegalia brevispica*

(b) *Vachellia drepanolobium*
Photo: G. N.Stone

(c) *Rhyncomya* (Calliphoridae) on
*Vachellia hockii* Photo: G. N. Stone

(d) Cerambycid beetle on
*Vachellia etbaica* Photo: G. N.Stone

(e) *Ceriana caffra* (Syrphidae) on *Senegalia mellifera*
Photo: A. Schnabel

Figure 2.9 Examples of flower heads of the Mpala acacia species.

(a) A view across Mpala to Mukenya

(b) The Turkana Boma plot used for web sampling

Figure 2.10 The habitat at Mpala

(a) *Solanum* sp. 1 (Solanaceae)

(b) *Commelina reptans* (Commelinaceae)

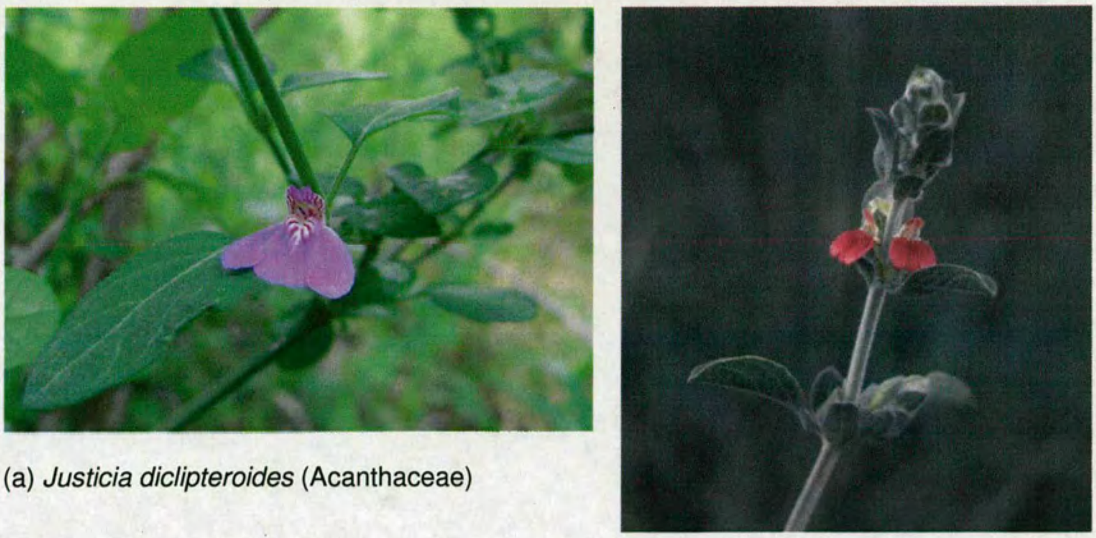
(c) *Carissa edulis* (Apocynaceae)

(d) *Gutenbergia cordifolia* (Asteraceae)

(e) *Ocimum forskolei* (Lamiaceae)

(f) *Kalanchoe* sp. 2 (Crassulaceae)

Figure 2.11 Examples of flowering plant species at Mpala



(a) *Justicia diclipteroides* (Acanthaceae)

(b) *Monechma* sp. B (Acanthaceae)

(c) *Abutilon mauritianum* (Malvaceae)

(d) *Sida ovata* (Malvaceae)

(e) *Ipomoea hildebrantii* (Convolvulaceae)

(f) *Hibiscus flavifolius* (Malvaceae)

Figure 2.12 Examples of flowering plant species at Mpala

(a) *Coryna* species (Meloidae) on *H. flavifolius*

(b) Colletid bee on *H. flavifolius*

(c) *Apis mellifera* (Apidae) on *C. reptans*

(d) *Pachnoda elegantissima* (Scarabaeidae) on *V. gerrardii*

(e) *Hylaeus* species (Colletidae) on *S. brevispica*

(f) *Apis mellifera* (Apidae) on *A. mauritianum*

Figure 2.13 Examples of flower visitors

# Chapter 3. Flowering phenologies of the Mpala acacia species

## Summary

The flowering phenologies of the ten acacia species at Mpala were examined twice per month between June 1999 and December 2005. Flowering was recorded using a qualitative four point scale. The majority of species had bimodal flowering phenologies, although *S. brevispica* had a trimodal flowering phenology. Co-flowering among large groups of acacia species was rare and occurred mainly among groups of between two and four species. *Senegalia brevispica*, *V. drepanolobium*, *V. gerrardii*, *V. nilotica* and *V. seyal* flowered for long periods each year and flowered most often with other acacias, although they co-flowered with different species between sites and years. Competition for pollination could exist among co-flowering acacias that shared pollinators.

In contrast to a study of acacias in Tanzania, where co-flowering occurred among up to eight acacia species sharing a relatively short flowering season, several of the Mpala acacias flowered for extended periods of time and, although co-flowering occurred among small groups of species, large groups of acacias did not regularly co-flower. It is suggested that the different patterns of flowering at Mpala could be due to a trimodal rainfall pattern, which is unusual in most parts of East Africa.

## 3.1 Introduction

Phenology is the study of the periodicity or seasonal timing of recurring biological events. In plant species the timing of flowering, fruiting and leafing cycles are important to survival and reproductive success. In this chapter I examine the flowering phenologies for the ten acacia species at Mpala to determine which acacias co-flower, and how frequently this occurs.

### 3.1.1 Why does flowering phenology matter with respect to competition for pollination?

Competition for pollination is thought to be an important force structuring flowering in plant communities (reviewed by Pleasants 1983, Rathcke 1983, Waser 1983). Competition can occur among plants through reduced numbers of pollinator visits or through heterospecific pollen transfer (Waser 1978a, b, Rathcke 1983). Species competing for pollination might diverge along some resource axis in order to minimise competition for pollination (see Chapter 1). Sympatric plant species that share pollinators could diverge in the seasonal timing of flowering to minimise overlap in flowering time, thereby reducing competition for pollination (e.g. Stiles 1977, Waser 1978a, Pleasants 1980, Ashton et al. 1988, Petanidou and Vokou 1993, Aizen and Vazquez 2006).

In seasonal habitats the availability of resources such as water, light or temperature can limit potential flowering seasons and plant species could be constrained to flower at similar times (Janzen 1967a, Hocking 1968, Reich and Borchert 1984, Johnson 1992). Co-flowering plant species that share pollinators could develop alternative strategies to minimise competition for pollination, tolerate competition, or facilitate pollination through local pollinator attraction (Schemske 1981, Thomson 1982). One way in which co-flowering plant species could minimise competition for shared pollinators is by segregating pollinator visits in daily time (Armbruster and Herzig 1984, Stone et al. 1996, 1998, Raine 2001). Stone et al. (1998) demonstrated that six co-flowering acacia species in a seasonal savannah habitat in Tanzania partitioned visits by shared pollinators in daily time through the divergence of dehiscence and pollen availability in daily time.

Therefore the consideration of species' flowering phenologies is important in the study of pollination interactions among plant species in order to understand the impact of flowering times on plant communities. Examination of flowering phenologies enables the identification of (i) species whose flowering seasons do not overlap and are thus unlikely to compete for pollinators, but that could facilitate each other's pollination by sustaining pollinator populations throughout the season and (ii) species that share flowering seasons and pollinators that could experience competition or facilitation of pollination through local pollinator attraction. If seasonal flowering times of sympatric plant species sharing pollinators are regularly spaced this could be evidence of resource partitioning in seasonal time, but further investigation would be necessary to determine whether this was due to competition for pollination.

### 3.1.2 What drives phenological patterns of flowering?

The flowering phenology of a plant species can be affected by a number of factors:

*(a) Environmental factors*

Local climatic factors will influence the seasonal flowering times of plant species. In temperate regions flowering seasons can be limited by temperature, with the majority of plants flowering during the spring and summer when the climate is warmer and pollinator species are more active (Rathcke and Lacey 1985). In tropical habitats the availability of light and water can influence flowering times (Opler et al. 1980, Augspurger 1982, van Schaik et al. 1993, Wright and van Schaik 1994). In seasonal tropical habitats rain falls during particular months of the year and flowering usually occurs at specific times in the wet/dry seasonal cycle (Frankie et al. 1974, Croat 1975, Milton 1987, Bullock and Solis-Magallanes 1990, Lobo et al. 2003). The ability of the soil to retain moisture during dry seasons can also affect water availability and the timing of flowering (Bullock and Solis-Magallanes 1990). In contrast, in aseasonal tropical forests, which retain moisture throughout the year and have no definite dry season, species tend to have irregular flowering patterns and often show less intra-specific synchrony in flowering (Putz 1979, Opler et al. 1980, Newstrom et al. 1994). Borchert et al. (2005) suggested that changes in photoperiod induce synchronous flowering in rainforests with low climatic seasonality in South

America, and in tropical rainforests in aseasonal southeast Asia, seasonal droughts have been proposed as triggers of simultaneous mass flowering at irregular intervals of two to ten years (Ashton et al. 1988, Appanah 1993, Sakai et al. 2006).

The timing of flowering could also be linked to the timing of other aspects of a plant's reproductive cycle, namely fruit production, seed dispersal and germination (Primack 1987). Flowering will precede this sequence and, whilst there can be time delays between stages, the optimal timing for subsequent processes may determine the timing of flowering.

*(b) Biotic factors*

The availability of suitable pollinators could affect the timing of flowering seasons, although it can be argued that pollinators time their activity to coincide with the availability of floral resources (Waser and Real 1979, Rathcke and Lacey 1985, van Schaik et al. 1993). Flowering could also be timed to ensure that fruiting occurs when appropriate seed dispersers are present or to avoid flower or seed predation (Rathcke and Lacey 1985, van Schaik et al. 1993, Brody 1997).

The influence of these biotic factors could lead to the maximisation or minimisation of overlap in flowering phenologies between species. Plant species sharing pollinators might compete for pollination and could minimise competition by reducing the length of time for which their flowering overlaps. A number of studies have found that plant species sharing pollinators flower sequentially or at different times of year, however only a handful of studies have shown flowering to be significantly regularly spaced in seasonal time, which would be consistent with a prediction of resource partitioning in seasonal time due to competitive displacement (Pleasants 1980, Gleeson 1981, Ashton et al. 1988, Prescott 2005, Aizen and Vazquez 2006).

Competition for pollinators is not the only plausible explanation for the occurrence of regularly spaced flowering in seasonal time. Sequential flowering among plant species that share pollinators could occur through an ecological sorting process that eliminates inferior competitors from communities resulting in the coexistence of plant species with minimal overlap (Moeller 2004). Sequential flowering could also help to maintain pollinator populations throughout a season and therefore benefit species sharing pollinators that flower at different times (e.g. Waser and Real 1979).

Although an overlap in seasonal flowering time could result in competition for pollinators, facilitation could also occur (Thomson 1982, Rathcke 1983). This could be particularly important for plant species growing at low densities, as a convergence in flowering time could result in increased pollinator attraction (Brown and Kodric-Brown 1979, Schemske 1981).

*(c) Phylogenetic conservatism*

Closely related plant species have been found to flower at similar times (Kochmer and Handel 1986, Johnson 1992, Wright and Calderon 1995). Plant species in the same genus, and to a lesser extent the same family, will inevitably share character traits that could restrict their seasonal flowering times. Kochmer and Handel (1986) examined the flowering times of the animal pollinated angiosperms in Japan and in two states in the United States (North and South Carolina) and found that most of the variation in flowering times could be explained by family membership. Furthermore, most families showed similar flowering times in the two locations. Wright and Calderon (1995) also found that plant species in the same genus, and to a lesser extent in the same family, on Barro Colorado Island in Panama shared similar flowering times.

Kochmer and Handel (1986) suggest that seasonal limitations of flowering times could be caused by phylogenetic constraints, which may not have changed for millions of years. If phylogenetic constraints are stronger than local selective pressures, members of the same taxa should have similar phenological patterns regardless of geographical location.

### 3.1.3 Flowering phenology studies of acacias and related species

Three studies have investigated the flowering phenologies of multi-species African acacia assemblages. In both Tanzania (Stone et al. 1998, Mduma et al. 2007) and South Africa (Milton 1987) groups of acacia species flowered simultaneously at particular times in the seasonal rainfall cycle. Stone et al. (1998) found that up to eight species co-flowered in December and January, after the main annual rains. More globally, Raine (2001) found that four acacia species in a seasonally dry forest in Mexico flowered at the end of the dry season and during the rainy season. The flowering phenologies of Australian acacias have been examined for arid-zone species in central and Western Australia (Davies 1976, Friedel et al. 1994) and species in southeastern temperate Australia (Prescott 2005). The findings of these studies will be described in more detail in the discussion.

The flowering phenologies of species in two other genera in the subfamily Mimosoideae have also been studied. Koptur (1983) examined the seasonal flowering patterns for seven species of *Inga* in Costa Rica. The genus *Inga* belongs to the tribe Ingaeae, to which recent phylogenetic studies suggest Australian acacias might be closely related (reviewed in Maslin et al. 2003, see Section 2.2.3). In Mexico, Camargo-Ricalde et al. (2004) investigated the flowering phenologies for a group of *Mimosa* species. The genus *Mimosa* is in the tribe Mimoseae and phylogenetic studies indicate that *Vachellia* is nested within the Mimoseae (see Section 2.2.3). The results of these studies will also be described further in the discussion.

### 3.1.4 Acacia flowering phenologies at Mpala

Given that acacia species in seasonal savannah habitats in Tanzania displayed high levels of co-flowering in response to rainfall, we might expect species growing in multi-acacia assemblages in the same habitat type in Kenya to demonstrate similar patterns of flowering. To establish the importance of seasonal flowering structure for the acacia community at Mpala I investigated the flowering phenology of each acacia species. By comparing these across species I aimed to establish (i) the extent of division of flowering over a seasonal timescale and (ii) the extent of co-flowering between acacias in this community. I also considered the effect of rainfall as a causal factor of acacia flowering patterns at this site. The aim of this study was not to quantify the absolute availability of floral resources in the community but simply to produce an accurate measure of species' flowering effort throughout the year to enable reliable comparisons in flowering times between species.

In this chapter I assess the potential for regular co-flowering groups of acacia species at Mpala by addressing the following questions:

1. What are the flowering phenologies of the Mpala acacia species?

(a) Does each species show a consistent pattern year to year in (i) modality of flowering and (ii) intensity of flowering?

(b) Do acacia species have similar flowering phenologies across study sites?

2. Do acacia species regularly co-flower at Mpala? Do the same species co-flower (a) across sites and (b) between years?

I also visually compare rainfall patterns throughout the study to the acacia flowering phenologies to examine the effect rainfall might have on flowering time.

## 3.2 Methods

### 3.2.1 Data collection

Flowering for the Mpala acacias was recorded twice per month from May 1998 until December 2005 at eight sites (Table 3.1). Data collection was initiated by Dr G. N. Stone (University of Edinburgh) and Professor P. G. Willmer (University of St Andrews), and data were collected by R. Eraguy from June 1999 until December 2005 with assistance from A. T. Watson, J. C. Ruiz Guajardo, P. Lenguya and J. Lima. Due to difficulties in data collection, sampling at the Mukenya site ceased in August 2003. Prior to June 1999 sampling was intermittent and therefore only data collected between June 1999 and December 2005 will be examined here. The total number of records available for each site is given in Table 3.1. For all sites except Mukenya and High Dam a continuous data set of 156 sampling points over 78 months was available for analysis. High Dam was not sampled between November 2004 and March 2005 due to problems with site access, hence the smaller number of sampling points for this site. Information regarding bud and pod availability was collected simultaneously, although these data will not be examined here.

Table 3.1. The numbers of individuals sampled for each acacia species and the number of sampling points per site. 1: MRC, 2: Turkana Boma, 3: Mongoose, 4: Mukenya, 5: Junction, 6: High Dam, 7: River, 8: Boma

| **Site** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **Total number of trees** |
|---|---|---|---|---|---|---|---|---|---|
| No. of sampling points | 156 | 156 | 156 | 101 | 156 | 145 | 156 | 156 | |
| *S. brevispica* | 10 | 10 | 10 | 10 | 10 | 10 | | | **60** |
| *V. drepanolobium* | | 10 | 10 | | 10 | | | | **30** |
| *V. etbaica* | 10 | 10 | | 10 | 10 | | | | **40** |
| *V. gerrardii* | | 10 | 10 | | 10 | 10 | | | **40** |
| *V. hockii* | | | | | 10 | 10 | | | **20** |
| *S. mellifera* | 10 | 10 | 10 | 10 | 10 | 10 | | | **60** |
| *V. nilotica* | 10 | 10 | | 10 | 10 | 10 | | | **50** |
| *V. seyal* var. *seyal* | | 10 | | | 10 | | | | **20** |
| *V. tortilis* | | | | | | | | 10 | **10** |
| *V. xanthophloea* | | | | | | | 10 | | **10** |
| **Total number of trees** | **40** | **70** | **40** | **40** | **80** | **50** | **10** | **10** | **350** |

The acacia species sampled at each of the eight sites are shown in Table 3.1. Further information regarding the sites can be found in Chapter 2. All acacia species present at each site were sampled, with the exception of Boma and River where only *V. tortilis* and *V. xanthophloea* were sampled respectively. At each site ten marked trees of each study species were sampled at approximately two week intervals at the start and in the middle of each calendar month.

Trees were scored for the presence of flowers on a four-point scale throughout the study period. The criteria for the categories on this scale are shown in Table 3.2. This method was intended to enable a qualitative comparison of trends in phenological patterns between years and sites and of variation in relative intensity of flowering. This in turn allowed the identification of which acacia species commonly co-flowered. However this method would not allow quantitative analysis of absolute variation in floral resource availability or direct comparison of flowering effort between species.

To calibrate flowering scores to absolute values, between November 2003 and December 2005 the number of flowers present on each tree was counted at the same time as the tree was scored on the four-point scale. This was used to assess the effectiveness of these categories to determine the consistency of the scale over the years in which data were collected. For the majority of species it was possible to count individual flower heads on a tree. However species such as *V. etbaica* and *S. mellifera* can produce large numbers of flowers at a time on a single tree making a total count very difficult. When these species were in full flower an estimation of the number of flowers present was calculated by counting an estimated representative fraction of the tree and multiplying up as necessary for the full canopy.

Table 3.2 Categories used to score flowering levels of acacia trees

| **Score** | **Interpretation** |
|---|---|
| 0 | no flowers |
| 1 | few flowers |
| 2 | moderate flowering or approx. half tree in full flower |
| 3 | tree in full flower |

### 3.2.2 Data analysis

*(a) Flowering phenologies of individual acacia species*

Flowering phenologies were examined for each species by comparing the data collected using the four-point scale between years. At each sampling point the mean flowering score of the ten marked trees was calculated for each species at each site. The mean flowering scores of each species were used to compare flowering modality (number of flowering peaks per year) and flowering intensity (amount of flowering) between years and between sites.

*(b) Identification of co-flowering acacia species*

Co-flowering species were identified for each site by comparing the mean flowering score of species at each sampling point. Since flowering intensity varied between species there was no minimum threshold flowering level for inclusion as a coflowering species; all species that were flowering at each sampling point were included. Only one acacia species' flowering phenology was recorded at Boma and River sites, therefore these sites were not considered in this analysis (Table 3.1).

All combinations of co-flowering species that occurred at each site were identified. The frequency with which each combination occurred was quantified by counting the number of sampling points for which the species co-flowered. This was expressed as a percentage of the total number of sampling points for that site (see

Table 3.1). Sites were compared to establish whether the same sets of species consistently co-flowered in different locations and between years.

*(c) Estimation of floral resources using quantified data*

The quantitative data collected for each category on the four point scale were examined for the species within each sampling site and for all sites combined. The range of flower numbers incorporated in each category on the scale were compared using the non-parametric Mann Whitney test in Minitab 14.0 as some data sets were not normally distributed. Since this is a non-parametric test this compared the median values of each category.

*(d) Local rainfall data*

Daily rainfall measurements were made by Mpala Research Centre throughout the study. These measurements were taken at the centre buildings, near to the MRC sampling site. Monthly rainfall totals were calculated and are presented to allow visual comparison with the acacia species' flowering phenologies. A formal statistical analysis of rainfall correlations with flowering phenologies is beyond the scope of this thesis.

## 3.3 Results

### 3.3.1 Flowering phenologies of the Mpala acacia species

In this section I describe the flowering phenologies of the Mpala acacia species. First I consider the variation across years for the entire dataset in terms of flowering modality and flowering intensity. I then consider the variation in flowering patterns between sampling sites.

*(a) Variation between years*

The overall flowering phenology for each species was calculated across years and sites (Fig. 3.1). Full data for each species over all years of the study are shown in Appendix 1. The months during which each acacia species flowered throughout the entire study are summarised in Table 3.3.

### *(i) Modality of flowering*

The majority of species had bimodal flowering phenologies (Fig. 3.1, Table 3.3). *Vachellia drepanolobium, V. etbaica, V. gerrardii, S. mellifera* and *V. nilotica* were clearly bimodal with two flowering peaks in most years (Appendix 1). *Vachellia hockii, V. tortilis* and *V. xanthophloea* had bimodal flowering phenologies, although did not flower during every year of the study (Fig. 3.1, Appendix 1).

The relative intensity of the two flowering peaks varied between species (Fig. 3.1, Appendix 1). For *V. drepanolobium* and *V. nilotica* the two flowering peaks were equally strong in most years. In *V. etbaica* the second flowering peak (August-October) was usually stronger than the first flowering peak (February-March). For *V. gerrardii* the first flowering peak (April-May) was stronger than the second (July-August) in the majority of years. In *S. mellifera* there was variation in the relative intensity of the two flowering peaks between years. The overall phenology data suggest that the second flowering peak for each of *V. hockii, V. tortilis* and *V. xanthophloea* may be stronger than the first peak.

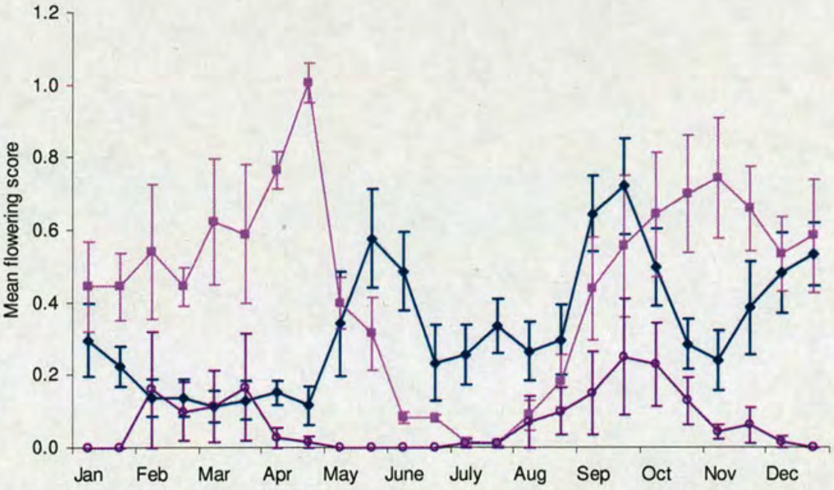
*Senegalia brevispica* had a trimodal flowering phenology and flowering peaks generally followed periods of high rainfall (Figs. 3.1, 3.2, Table 3.3). It is not clear whether *V. seyal* had a bimodal or trimodal flowering pattern as the number of flowering peaks varied between years (Appendix 1).

### *(ii) Intensity of flowering*

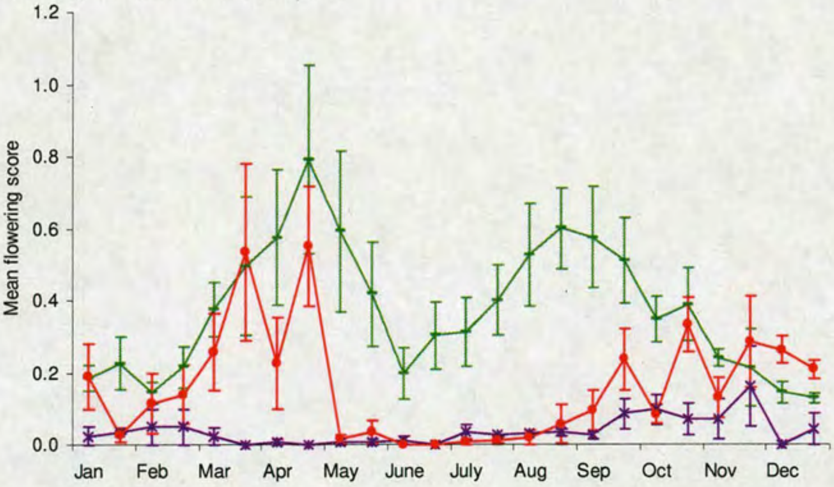
*Senegalia brevispica, V. drepanolobium, V. etbaica, V. gerrardii, S. mellifera* and *V. nilotica* all had relatively high intensities of flowering (Fig. 3.1). The flowering intensities of *V. hockii, V. seyal, V. tortilis* and *V. xanthophloea* were relatively low, although *V. tortilis* occasionally had larger flowering peaks (Fig. 3.1, Appendix 1).

Flowering intensity varied between years in a number of species (Appendix 1). *Senegalia brevispica* flowered at much lower levels in 2000 than in any other year. Flowering intensity was also greater between 2001 and 2003 than in 2004 and 2005 (Appendix 1). Similar patterns of between-year variation were shown by *Vachellia drepanolobium, V. etbaica, V. nilotica* and *V. seyal* which flowered less intensely in 2004 and 2005 than in the preceding years.

*(a) S. brevispica, V. drepanolobium, V. tortilis*



*(b) V. gerrardii, V. hockii, S. mellifera*



*(c) V. etbaica, V. nilotica, V. seyal, V. xanthophloea*

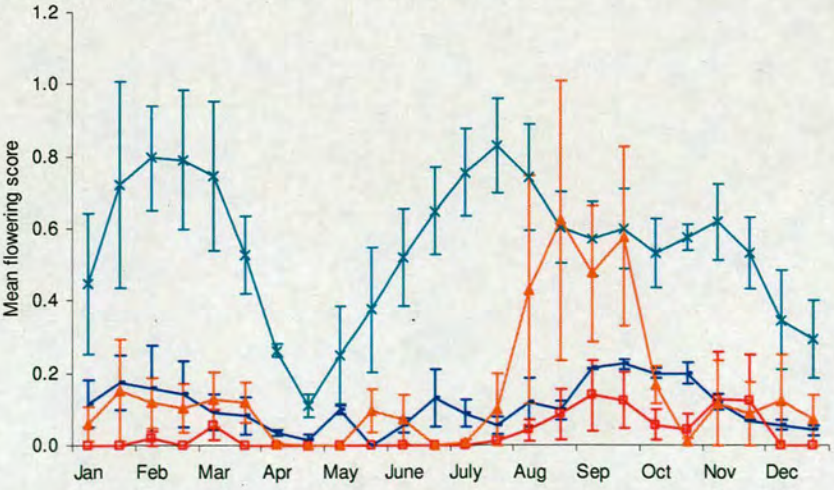


Figure 3.1 Mean flowering scores for each acacia species across sites and years (June 1999-December 2005) (± 1SE).

Key to species:
◆ brevispica
■ drepanolobium
▲ etbaica
— gerrardii
✱ hockii
● mellifera
+ nilotica
– seyal
○ tortilis
□ xanthophloea

Table 3.3 Typical flowering intensity of acacia species throughout the year. + indicates high flowering intensity, * indicates slight scattered flowering, - indicates a very low intensity of flowering (e.g. one tree producing a small number of flowers during that month). The columns shaded in blue indicate the months that, on average, received the most rainfall (see Fig. 3.2 for mean rainfall for each month).

| Acacia species | J | F | M | A | M | J | J | A | S | O | N | D | No. of peaks |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *S. brevispica* | + | * | * | * | + | + | * | * | + | + | * | + | 3 |
| *V. drepanolobium* | * | + | + | + | * | * | - | * | + | + | + | + | 2 |
| *V. etbaica* | + | + | + |  | * | * | * | + | + | + | + | + | 2 |
| *V. gerrardii* | * | * | + | + | + | * | + | + | + | + | * | * | 2 |
| *V. hockii* | * | + | * | - | - | - | * | * | + | + | + | * | 2 |
| *S. mellifera* | * | * | + | + | * |  | - | * | + | + | + | + | 2 |
| *V. nilotica* | + | + | + | * | * | + | + | + | + | + | + | * | 2 |
| *V. seyal* | + | + | * | - | - | + | * | * | + | + | * | * | 2/3 |
| *V. tortilis* |  | + | + | * |  |  | - | + | + | + | * | - | 2 |
| *V. xanthophloea* |  | - | * |  |  |  | - | * | + | * | + |  | 2 |

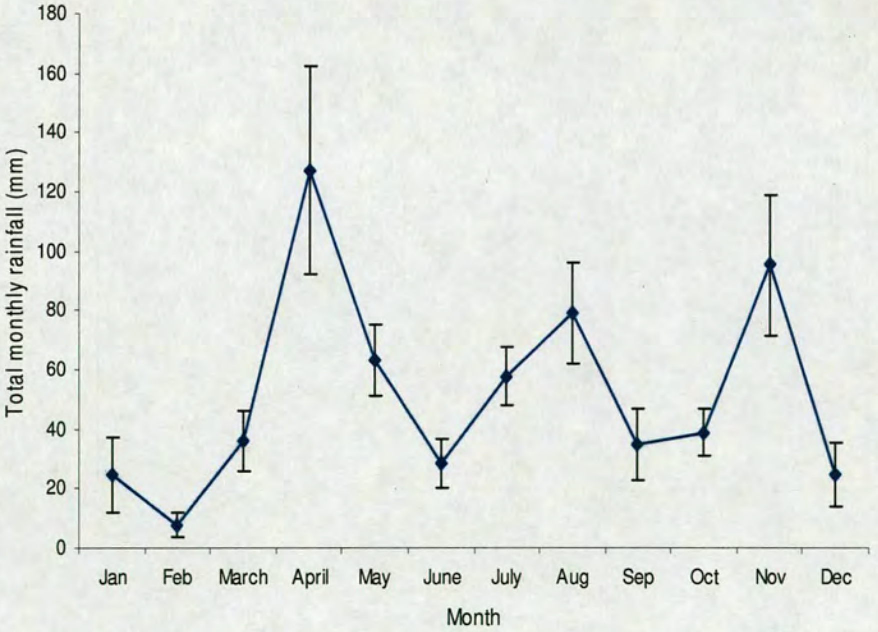


Figure 3.2 Mean monthly total rainfall (± 1SE) at Mpala Research Centre between May 1998 and December 2005 (readings taken near to MRC site). The full data for all months are shown in Appendix 3.3.

### *(b) Variation between sites*

All species except *V. tortilis* and *V. xanthophloea* were sampled at multiple sites. The flowering phenologies for the acacia species at each site are shown in Figure 3.3. Full data for each species over all years of the study are shown in Appendix 2.

### *(i) Modality of flowering*

*Vachellia drepanolobium*, *V. gerrardii*, *S. mellifera* and *V. nilotica* showed bimodal flowering phenologies at all sites (Fig. 3.3, Appendix 2), although dates of flowering seasons in individual years often varied between sites. *Senegalia brevispica* had a trimodal flowering pattern at all sites in most years.

*Vachellia etbaica* had a bimodal flowering phenology at most sites (Fig. 3.3), although flowering rarely occurred twice in each year at any site (Appendix 2). The *V. etbaica* trees at Junction flowered extremely rarely during the entire study.

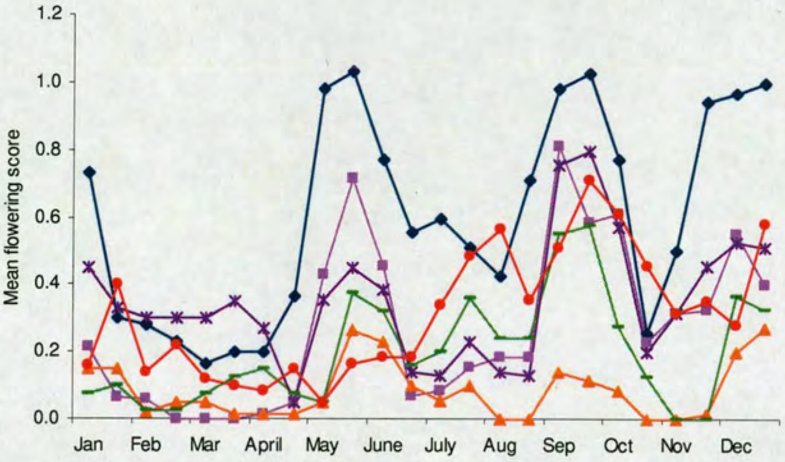
*Vachellia seyal* had different flowering patterns at the two sites at which it was sampled. The pattern over all years was trimodal at Junction but bimodal at Turkana Boma (Fig. 3.3). At both sites the number of flowering peaks varied between years.

The flowering patterns for *V. hockii* varied between Junction and High Dam, although at both sites flowering was approximately bimodal (Fig. 3.3). *Vachellia hockii* did not show consistent flowering patterns between years at either site and flowering rarely occurred simultaneously at the two sites (Appendix 2).

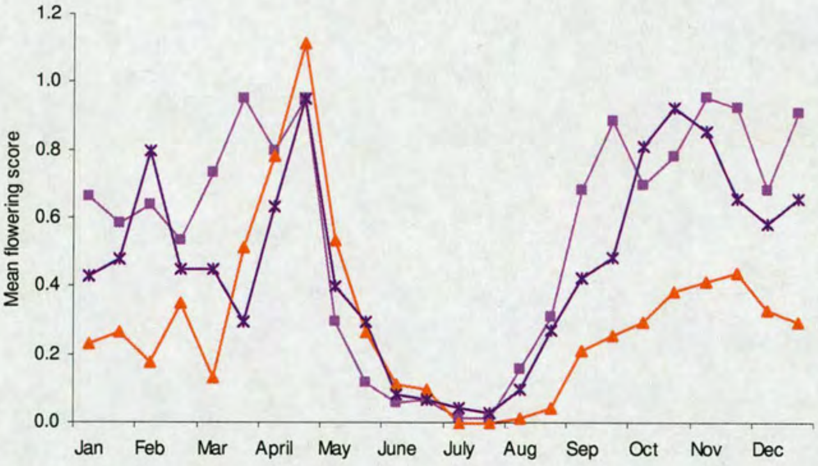
### *(ii) Intensity of flowering*

Flowering intensity for most species varied between sites (Fig. 3.3, Appendix 2). For example, the *S. brevispica* trees at MRC often flowered more strongly than trees at other sites whereas those at Mongoose usually flowered least strongly (Fig. 3.3). *Vachellia gerrardii* flowered with greatest intensity at High Dam and with least intensity at Mongoose (Fig. 3.3). Species at one site were not consistently lower than all species at another site, although flowering intensity was relatively high for most species at Mukenya and relatively low for several species at Mongoose.

*(a) S. brevispica*



*(b) V. drepanolobium*



*(c) V. etbaica*

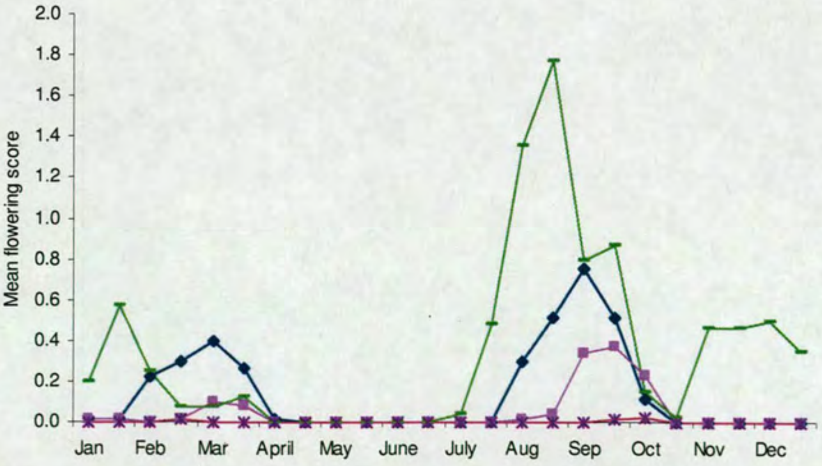
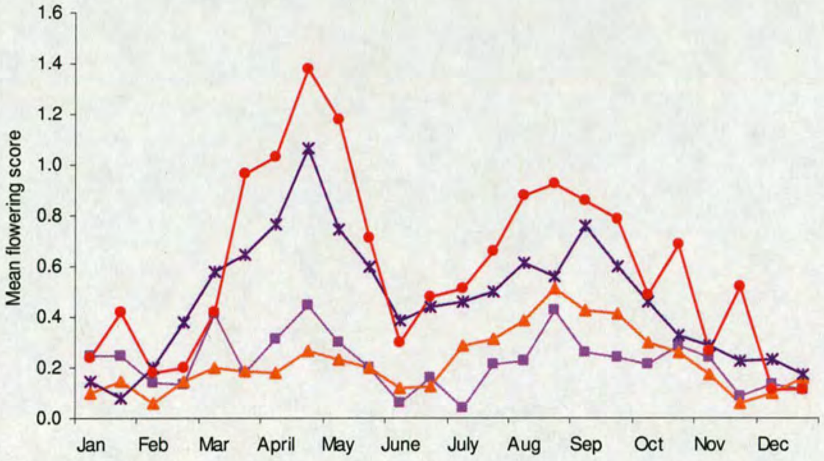


Figure 3.3 Mean flowering scores across years for each acacia species at each site.

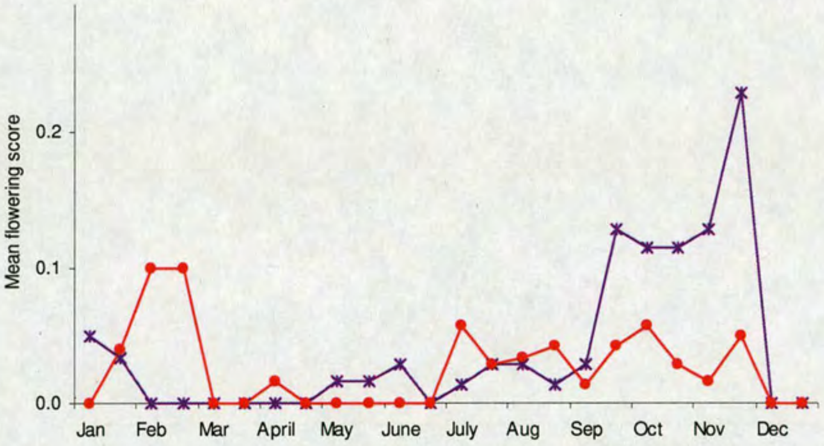
Key to sites:

| | |
|---|---|
| —◆— MRC | —▬— Mukenya |
| —■— Turkana Boma | —✱— Junction |
| —▲— Mongoose | —●— High Dam |

(d) *V. gerrardii*



*(e) V. hockii*



*(f) S. mellifera*

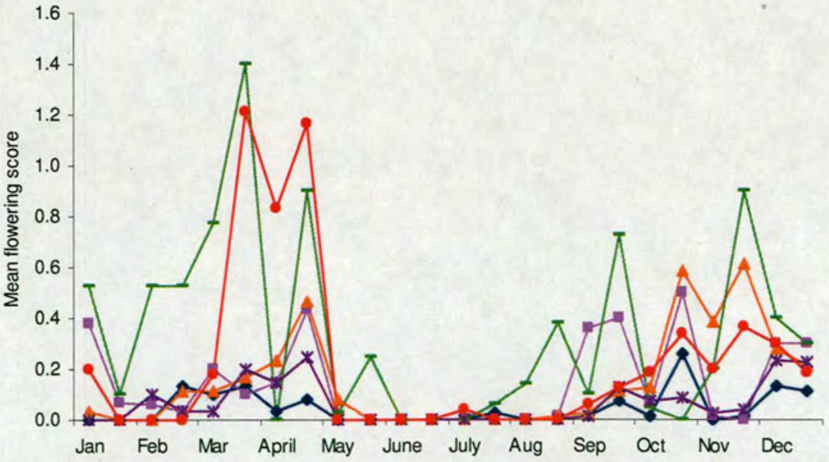
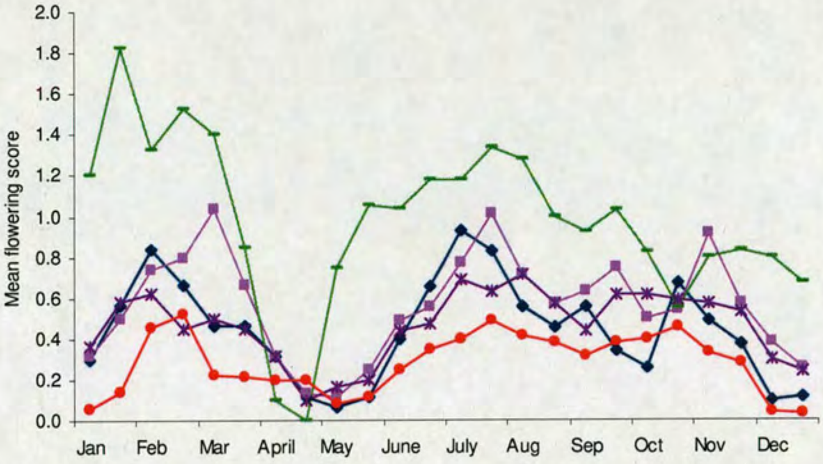


Figure 3.3 (cont.) Mean flowering scores across years for each acacia species at each site.

Key to sites:
—◆— MRC
—■— Turkana Boma
—▲— Mongoose
—— Mukenya
—✱— Junction
—●— High Dam

*(g) V. nilotica*



*(h) V. seyal*

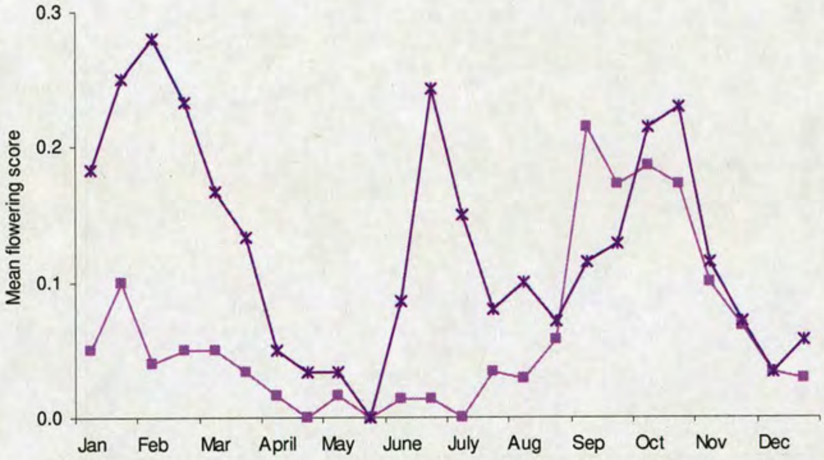


Figure 3.3 (cont.) Mean flowering scores across years for each acacia species at each site.

Key to sites:
—◆— MRC
—■— Turkana Boma
—▲— Mongoose
—— Mukenya
—✱— Junction
—●— High Dam

### 3.3.2 Co-flowering acacia species

Selection can affect how species co-flower in space and time. A feature of the Mpala data is that (i) species combinations vary across sites, and (ii) flowering phenologies of species to some extent vary across sites and years. The aim of this section is not to explain this variation in detail, but to extract general patterns for the Mpala system and specifically which combinations of species most often co-flower.

In this section I first illustrate co-flowering species at each site, using mean data across years (Fig. 3.4). Full data for all years at each site are given in Appendix

4. I then summarise the extent to which specific sets of acacias co-flowered across sites. Full data on the frequency of co-flowering between specific species sets at each site are given in Appendix 5.

Sites with a greater richness of acacia species can obviously support a greater number of potential co-flowering acacia sets. Thus more complex potential interactions are possible at Turkana Boma and Junction, with seven and eight species respectively, than at MRC, Mongoose and Mukenya, which had only four species. A further feature of the Mpala data is that (as shown in Section 3.3.1) some acacias flowered more often and for longer than others, and these had the greatest potential for co-flowering. For these reasons, the most commonly co-flowering species across Mpala as a whole were *S. brevispica*, *V. drepanolobium*, *V. gerrardii*, *V. nilotica* and *V. seyal*. *Vachellia etbaica*, *V. hockii* and *S. mellifera* flowered less frequently and therefore the time for which they could potentially co-flower was smaller in comparison to the other species. Finally, co-flowering between pairs of species is much more common, unsurprisingly, than between larger sets of species. I first consider specific co-flowering species pairs, before discussing larger sets of co-flowering species.

### *(a) Pairs of co-flowering species*

Across sites and years the most frequently co-flowering species pairs were combinations of *S. brevispica*, *V. drepanolobium*, *V. gerrardii* and *V. nilotica* (Table 3.4, Appendix 5). The frequency with which the most common species pair co-flowered at each site ranged from 29% at Mongoose (*V. drepanolobium* and *V. gerrardii*) to 60% of sampling points at High Dam (*V. gerrardii* and *V. nilotica*) (Table 3.4).

The next most frequent co-flowering species was *V. seyal* which, although flowering at low intensity, flowered relatively frequently and hence overlapped with other acacias at the two sites where it was present. *Vachellia seyal* flowered most often with *V. nilotica* at both Turkana Boma and Junction (31% and 37% of sampling points respectively), but also commonly with *S. brevispica*, *V. drepanolobium* and *V. gerrardii* during most years of the study (Table 3.4, Appendix 5).

*Senegalia mellifera* co-flowered most often with *V. drepanolobium* at Turkana Boma and Mongoose (18% and 17% of sampling points respectively), *V.*

*gerrardii* at Junction and High Dam (12% and 23% of sampling points respectively) and *V. nilotica* at Mukenya (26% of sampling points) (Table 3.4). These pairs of species co-flowered during most years of the study. At MRC *S. mellifera* rarely co-flowered with the other species, flowering with other acacias for less than 5% of sampling points (Appendix 5).

*Vachellia etbaica* flowered most often with *S. brevispica* at Mpala (16% of sampling points) and with *V. nilotica* at Turkana Boma and Mukenya (12% and 30% of sampling points respectively) (Table 3.4). These species combinations occurred during most years of the study. *Vachellia etbaica* flowered rarely at Junction but co-flowered most often with *V. gerrardii* and *V. nilotica* (3% of sampling points) in 2003, 2004 and 2005 (Appendix 5).

*Vachellia hockii* flowered less often than most of the other species at Junction and High Dam and co-flowered most frequently with *V. nilotica* at both sites in all years (15% and 27% of sampling points respectively) (Table 3.4).

### *(b) Groups of three co-flowering species*

The most frequently co-flowering sets of three species across sites also involved *S. brevispica*, *V. drepanolobium*, *V. gerrardii* and *V. nilotica* (Table 3.4). Co-flowering occurred most frequently between *S. brevispica*, *V. gerrardii* and *V. nilotica* at High Dam (34% of sampling points) and *V. drepanolobium*, *V. gerrardii* and *V. nilotica* at Junction and Turkana Boma (41% and 31% of sampling points respectively) (Table 3.4). Three-way co-flowering was less frequent overall at MRC, Mongoose and Mukenya where it involved combinations of *S. brevispica*, *V. drepanolobium*, *V. etbaica*, *V. gerrardii*, *S. mellifera* and *V. nilotica* (Table 3.4).

### *(c) Groups of four co-flowering species*

Groups of four co-flowering species were rare at MRC and Mongoose (1-2% of sampling points) and occurred only slightly more often at Mukenya (8% of sampling points) (Table 3.4). At High Dam *S. brevispica*, *V. gerrardii*, *S. mellifera* and *V. nilotica* co-flowered for 11% of sampling points and this combination occurred in most years (Table 3.4, Appendix 5). Other combinations of four co-flowering species at this site were rare and did not regularly occur (Table 3.4, Appendix 5). Groups of four co-flowering species occurred more frequently at

Turkana Boma and Junction with the most common combination at Turkana Boma (*V. drepanolobium*, *V. gerrardii*, *V. nilotica* and *V. seyal*) co-flowering for 15% of sampling points and in all years of the study (Table 3.4, Appendix 5). At Junction the most common combination (*S. brevispica*, *V. drepanolobium*, *V. gerrardii* and *V. nilotica*) occurred for 25% of sampling points and across all years (Table 3.4, Appendix 5). Several other sets of four co-flowering species were found less often at both sites (Table 3.4, Appendix 5).

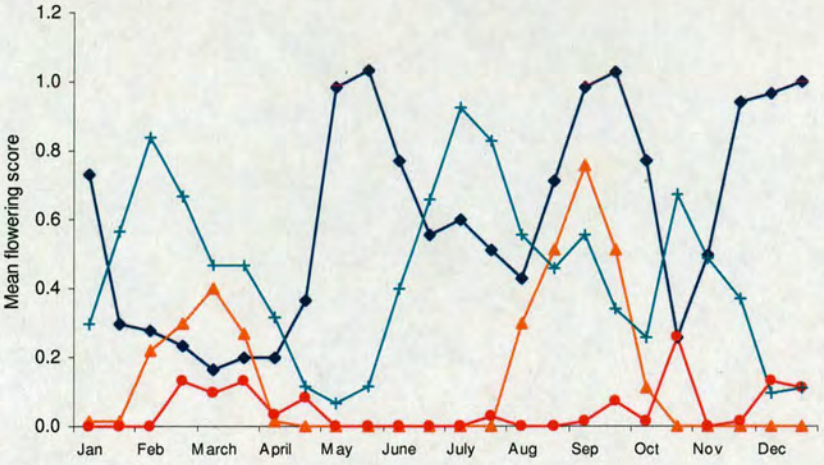
### *(d) Groups of five to seven co-flowering species*

At High Dam all five acacia species flowered together for only 2% of sampling points (Table 3.4). At both Turkana Boma and Junction the same five species (*S. brevispica*, *V. drepanolobium*, *V. gerrardii*, *V. nilotica* and *V. seyal*) co-flowered most frequently (for 8% of sampling points at Turkana Boma and 13% at Junction) (Table 3.4). This combination was found in most years of the study at both sites (Appendix 5). Several other groups of five species co-flowered at both sites for 6% of sampling points, but none was found consistently in all years of the study (Table 3.4, Appendix 5).

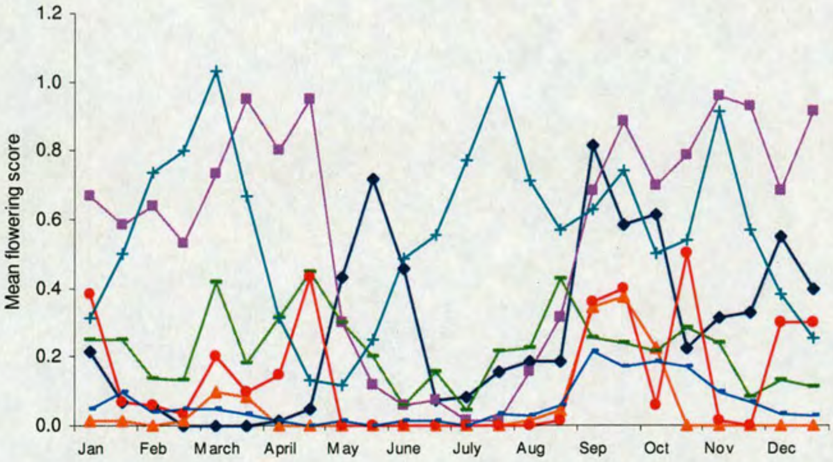
Larger groups of co-flowering species were extremely rare at both Turkana Boma and Junction. At Junction one combination of six species co-flowered in 1999, 2001 and 2003 for a total of 4% of sampling points, and four six-species combinations co-flowered for only 1% of sampling points (Table 3.4). No combinations of seven or eight species co-flowered at this site. At Turkana Boma two groups of six co-flowering species occurred for 4% of sampling points (Table 3.4). Each of these was found during three years of the study (Appendix 5). All seven species at Turkana Boma flowered together for 3% of sampling points in 2001 and 2004 (Table 3.4, Appendix 5).

Regular co-flowering by multiple acacias was rare at Mpala. The most frequent interactions involved small numbers of species (two or three), and although a consistent set of species was involved in more interactions (*S. brevispica*, *V. drepanolobium*, *V. gerrardii*, *V. nilotica* and *V. seyal*), the relative abundance of specific interactions varied across sites and years. There is no strong evidence for highly structured multi-species co-flowering at Mpala.

(a) Mpala



(b) Turkana Boma



(c) Mongoose

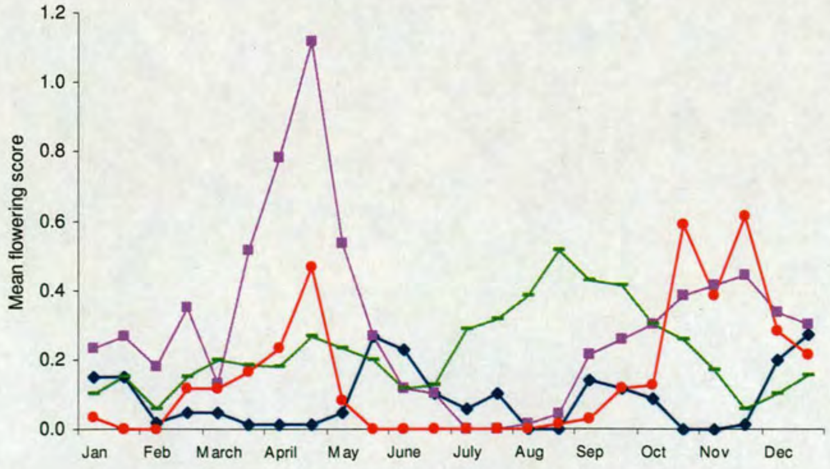
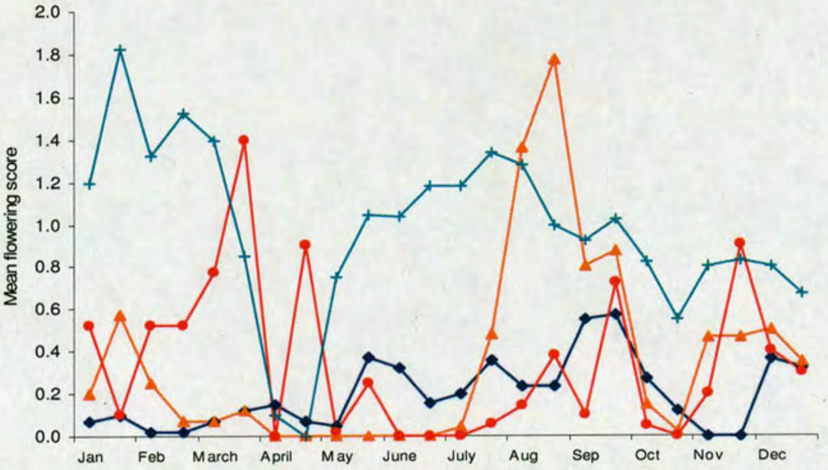


Figure 3.4 Mean flowering scores across years for all acacia species sampled at each site.

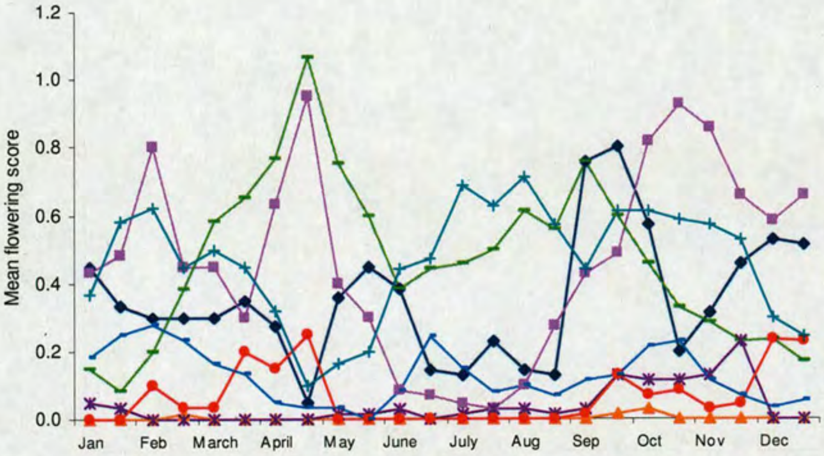
Key to species:

- ◆ brevispica
- ■ drepanolobium
- ▲ etbaica
- — gerrardii
- ✱ hockii
- ● mellifera
- + nilotica
- – seyal

(d) Mukenya



(e) Junction



(f) High Dam

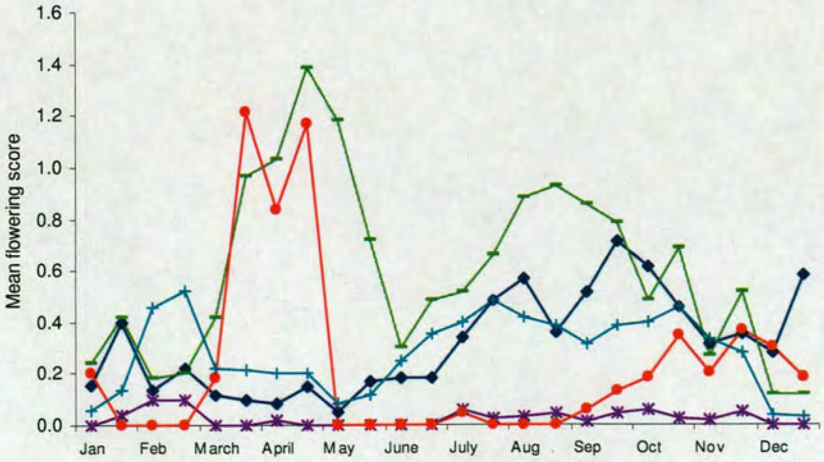


Figure 3.4 (cont.) Mean flowering scores across years for all acacia species sampled at each site.

Key to species:
- brevispica
- drepanolobium
- etbaica
- gerrardii
- hockii
- mellifera
- nilotica
- seyal

Table 3.4 The most frequently occurring combinations of co-flowering acacia species at each site and the percentage of sampling points for which they occur. For groups of two and three co-flowering species, combinations present for 10% or more of sampling points are shown. For groups of four to seven species the most frequently observed combinations of co-flowering species are shown. The species present at each site are shown below the site name. b: *S. brevispica*, d: *V. drepanolobium*, e: *V. etbaica*, g: *V. gerrardii*, h: *V. hockii*, m: *S. mellifera*, n: *V. nilotica*, s: *V. seyal*

| | MRC | % | Turkana Boma | % | Mongoose | % | Mukenya | % | Junction | % | High Dam | % |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | bemn | | bdegmns | | bdgm | | bemn | | bdeghmns | | bghmn | |
| Pairs of species | bn | 47 | dn | 54 | dg | 29 | bn | 30 | gn | 55 | gn | 60 |
| | be | 16 | dg | 37 | dm | 17 | en | 30 | dg | 52 | bn | 46 |
| | en | 15 | gn | 37 | gm | 14 | mn | 26 | dn | 51 | bg | 38 |
| | | | ns | 31 | | | em | 21 | bn | 46 | gm | 23 |
| | | | bn | 29 | | | be | 12 | bd | 43 | mn | 20 |
| | | | ds | 29 | | | bm | 10 | bg | 43 | hn | 27 |
| | | | bd | 24 | | | | | ns | 37 | bh | 14 |
| | | | bg | 19 | | | | | bs | 31 | bm | 13 |
| | | | dm | 18 | | | | | gs | 30 | gh | 10 |
| | | | bs | 17 | | | | | ds | 28 | | |
| | | | gs | 17 | | | | | hn | 15 | | |
| | | | mn | 17 | | | | | gh | 14 | | |
| | | | gm | 13 | | | | | dh | 13 | | |
| | | | en | 12 | | | | | gm | 12 | | |
| | | | | | | | | | hs | 11 | | |
| | | | | | | | | | dm | 10 | | |
| | | | | | | | | | bh | 10 | | |
| Three species | ben | 13 | dgn | 31 | dgm | 10 | emn | 20 | dgn | 41 | bgn | 34 |
| | | | dns | 24 | | | ben | 14 | bdn | 33 | gmn | 18 |
| | | | bdg | 18 | | | bmn | 10 | bgn | 33 | bgm | 13 |
| | | | dgm | 17 | | | | | bdg | 31 | bhn | 13 |
| | | | bdn | 16 | | | | | gns | 28 | bmn | 12 |
| | | | gns | 16 | | | | | dns | 25 | ghn | 10 |
| | | | dgs | 16 | | | | | dgs | 22 | | |
| | | | dmn | 15 | | | | | bgs | 21 | | |
| | | | bgn | 14 | | | | | bns | 20 | | |
| | | | bds | 12 | | | | | bds | 19 | | |
| | | | gmn | 12 | | | | | ghn | 13 | | |
| | | | | | | | | | dhn | 12 | | |
| | | | | | | | | | bhn | 10 | | |
| | | | | | | | | | dgm | 10 | | |
| | | | | | | | | | dgh | 10 | | |
| | | | | | | | | | hns | 10 | | |
| Four species | bemn | 2 | dgns | 15 | bdgm | 1 | bemn | 8 | bdgn | 25 | bgmn | 11 |
| | | | bdgn | 12 | | | | | dgns | 20 | bghn | 7 |
| | | | dgmn | 12 | | | | | bgns | 18 | | |
| | | | bdns | 10 | | | | | bdns | 16 | | |
| | | | | | | | | | bdgs | 14 | | |
| Five to seven species | | | bdgns | 8 | | | | | bdgns | 13 | bghmn | 2 |
| | | | dgmns | 6 | | | | | dghns | 6 | | |
| | | | bdens | 6 | | | | | bghns | 6 | | |
| | | | bdegns | 4 | | | | | bdghns | 4 | | |
| | | | degmns | 4 | | | | | | | | |
| | | | bdegmns | 3 | | | | | | | | |

### 3.3.3 Assessment of scoring categories using quantitative data

For the majority of species, each category in the four-point scale that was used to qualitatively assess flowering phenology represented significantly different numbers of flowers, although there was variation between species in terms of the range of flower numbers to which each category corresponded (Fig. 3.5, Table 3.5). For example, for *S. mellifera*, which can produce vast numbers of flowers at once, category 3 incorporated quantitative flower counts ranging from 300 up to an estimated 40,000 flowers, whilst for *S. brevispica* the same category represented counts of between 220 and 500 flowers. There was no significant difference between categories 2 and 3 in *V. drepanolobium* (Fig. 3.5), although both the mean and median values for category 3 were slightly higher (Table 3.5, Fig. 3.5). Trees of this species were scored in category 3 at Turkana Boma and Junction. At both sites the quantitative flower counts fell within the range incorporated by category 2. However since few trees were scored as category 3 (three at Turkana Boma and two at Junction) this discrepancy should not affect interpretation of the data.

The number of flowering events for *V. hockii*, *V. tortilis* and *V. xanthophloea* during the two years over which flowers were quantified was not large enough to determine the full range of all three categories for these species. The number of flowers produced by *V. hockii* and *V. xanthophloea* trees at any sampling point during this time did not exceed category 1. Similarly, the number of category 2 and 3 classifications for *V. seyal* was not sufficient to effectively compare the three categories for this species.

The variation for each species between sites was small (Table 3.5). Flowering levels at some sites were noticeably lower than at other sites and therefore the categories represented slightly different species ranges. For example, the mean number of flowers per category for three of the four species at Mongoose was smaller than those of the same species at other sites. However when the data from all sites were combined this did not affect the overall data ranges for each category.

Table 3.5 Sample size (N), mean and 95% confidence intervals (CI) for quantitative count data for each site and across all sites corresponding to the categories used to score flower presence in the long term phenology dataset.

*(a) S. brevispica*

| Category | 1 | | | 2 | | | 3 | | |
|---|---|---|---|---|---|---|---|---|---|
| | N | Mean | 95% CI | N | Mean | 95% CI | N | Mean | 95% CI |
| MRC | 147 | 21 | 15, 26 | 19 | 140 | 94, 185 | 6 | 381 | 265, 496 |
| Turkana | 90 | 8 | 6, 10 | 2 | 22 | 0, 124 | - | | |
| Mongoose | 18 | 3 | 2, 4 | 1 | 17 | 6, 9 | - | | |
| Junction | 123 | 7 | 6, 9 | 11 | 90 | 25, 155 | - | | |
| High Dam | 88 | 8 | 6, 9 | 1 | 25 | - | - | | |
| Overall | 466 | 11 | 10, 13 | 34 | 110 | 76, 143 | 6 | 381 | 265, 496 |

*(b) V. drepanolobium*

| Category | 1 | | | 2 | | | 3 | | |
|---|---|---|---|---|---|---|---|---|---|
| | N | Mean | 95% CI | N | Mean | 95% CI | N | Mean | 95% CI |
| Turkana | 87 | 18 | 14, 23 | 19 | 132 | 98, 166 | 3 | 140 | 0, 303 |
| Mongoose | 99 | 6 | 5, 8 | 5 | 65 | 0, 152 | - | | |
| Junction | 137 | 9 | 7, 10 | 8 | 76 | 38, 113 | 2 | 101 | 140, 342 |
| Overall | 323 | 18 | 9, 12 | 32 | 107 | 82, 132 | 5 | 124 | 59, 190 |

*(c) V. etbaica*

| Category | 1 | | | 2 | | | 3 | | |
|---|---|---|---|---|---|---|---|---|---|
| | N | Mean | 95% CI | N | Mean | 95% CI | N | Mean | 95% CI |
| MRC | 36 | 68 | 12, 125 | 6 | 152 | 126, 179 | 7 | 442 | 214, 671 |
| Turkana | 19 | 11 | 5, 18 | - | | | - | | |
| Junction | 3 | 27 | 0, 128 | - | | | - | | |
| Overall | 58 | 48 | 13, 83 | 6 | 152 | 126, 179 | 7 | 442 | 214, 671 |

*(d) V. gerrardii*

| Category | 1 | | | 2 | | | 3 | | |
|---|---|---|---|---|---|---|---|---|---|
| | N | Mean | 95% CI | N | Mean | 95% CI | N | Mean | 95% CI |
| Turkana | 41 | 14 | 10, 18 | 1 | 200 | - | - | | |
| Mongoose | 58 | 11 | 8, 13 | - | | | 2 | 169 | 0, 1198 |
| Junction | 86 | 29 | 18, 40 | 16 | 176 | 120, 233 | 12 | 427 | 340, 514 |
| High Dam | 72 | 25 | 13, 37 | 27 | 190 | 133, 247 | 9 | 877 | 377, 1376 |
| Overall | 257 | 21 | 16, 27 | 44 | 185 | 146, 225 | 23 | 580 | 374, 787 |

*(e) V. hockii*

| Category | 1 | | | 2 | | | 3 | | |
|---|---|---|---|---|---|---|---|---|---|
| | N | Mean | 95% CI | N | Mean | 95% CI | N | Mean | 95% CI |
| Turkana | 2 | 4 | 0, 8 | - | | | - | | |
| Junction | 2 | 2 | 0, 17 | - | | | - | | |
| Overall | 4 | 3 | 0, 6 | - | | | - | | |

Table 3.5 (cont.) Sample size (N), mean and 95% confidence intervals (CI) for quantitative count data for each site and across all sites corresponding to the categories used to score flower presence in the long term phenology dataset.

*(f) S. mellifera*

| Category | 1 | | | 2 | | | 3 | | |
|---|---|---|---|---|---|---|---|---|---|
| | N | Mean | 95% CI | N | Mean | 95% CI | N | Mean | 95% CI |
| Mpala | 17 | 61 | 0, 128 | 4 | 181 | 143, 219 | 1 | 650 | - |
| Turkana | 19 | 32 | 8, 56 | 8 | 104 | 70, 139 | 2 | 1173 | 0, 7869 |
| Mongoose | 35 | 35 | 20, 50 | 12 | 116 | 86, 147 | - | | |
| Junction | 20 | 19 | 13, 25 | 4 | 127 | 33, 222 | 2 | 520 | 0, 2045 |
| High Dam | 24 | 17 | 10, 24 | 11 | 355 | 111, 599 | 13 | 8595 | 504, 16,685 |
| Overall | 115 | 32 | 21, 43 | 39 | 189 | 118, 260 | 18 | 6432 | 539, 12,305 |

*(g) V. nilotica*

| Category | 1 | | | 2 | | | 3 | | |
|---|---|---|---|---|---|---|---|---|---|
| | N | Mean | 95% CI | N | Mean | 95% CI | N | Mean | 95% CI |
| Mpala | 151 | 9 | 7, 10 | 13 | 60 | 33, 87 | 1 | 270 | - |
| Turkana | 139 | 10 | 8, 13 | 10 | 163 | 80, 247 | - | | |
| Junction | 135 | 8 | 6, 11 | 17 | 83 | 52, 114 | - | | |
| High Dam | 63 | 13 | 8, 18 | 11 | 54 | 19, 89 | - | | |
| Overall | 488 | 9 | 8, 11 | 51 | 86 | 64, 109 | 1 | 270 | - |

*(h) V. seyal*

| Category | 1 | | | 2 | | | 3 | | |
|---|---|---|---|---|---|---|---|---|---|
| | N | Mean | 95% CI | N | Mean | 95% CI | N | Mean | 95% CI |
| Turkana | 40 | 9 | 6, 12 | 3 | 94 | 0, 279 | 1 | 55 | - |
| Junction | 25 | 4 | 2, 5 | 1 | 38 | - | 1 | 109 | - |
| Overall | 65 | 7 | 5, 9 | 4 | 80 | 0, 187 | 2 | 82 | 0, 425 |

*(i) V. tortilis*

| Category | 1 | | | 2 | | | 3 | | |
|---|---|---|---|---|---|---|---|---|---|
| | N | Mean | 95% CI | N | Mean | 95% CI | N | Mean | 95% CI |
| Boma | 13 | 43 | 14, 72 | 3 | 96 | 0, 320 | 1 | 246 | - |

*(j) V. xanthophloea*

| Category | 1 | | | 2 | | | 3 | | |
|---|---|---|---|---|---|---|---|---|---|
| | N | Mean | 95% CI | N | Mean | 95% CI | N | Mean | 95% CI |
| River | 2 | 2 | 0, 8 | - | | | - | | |

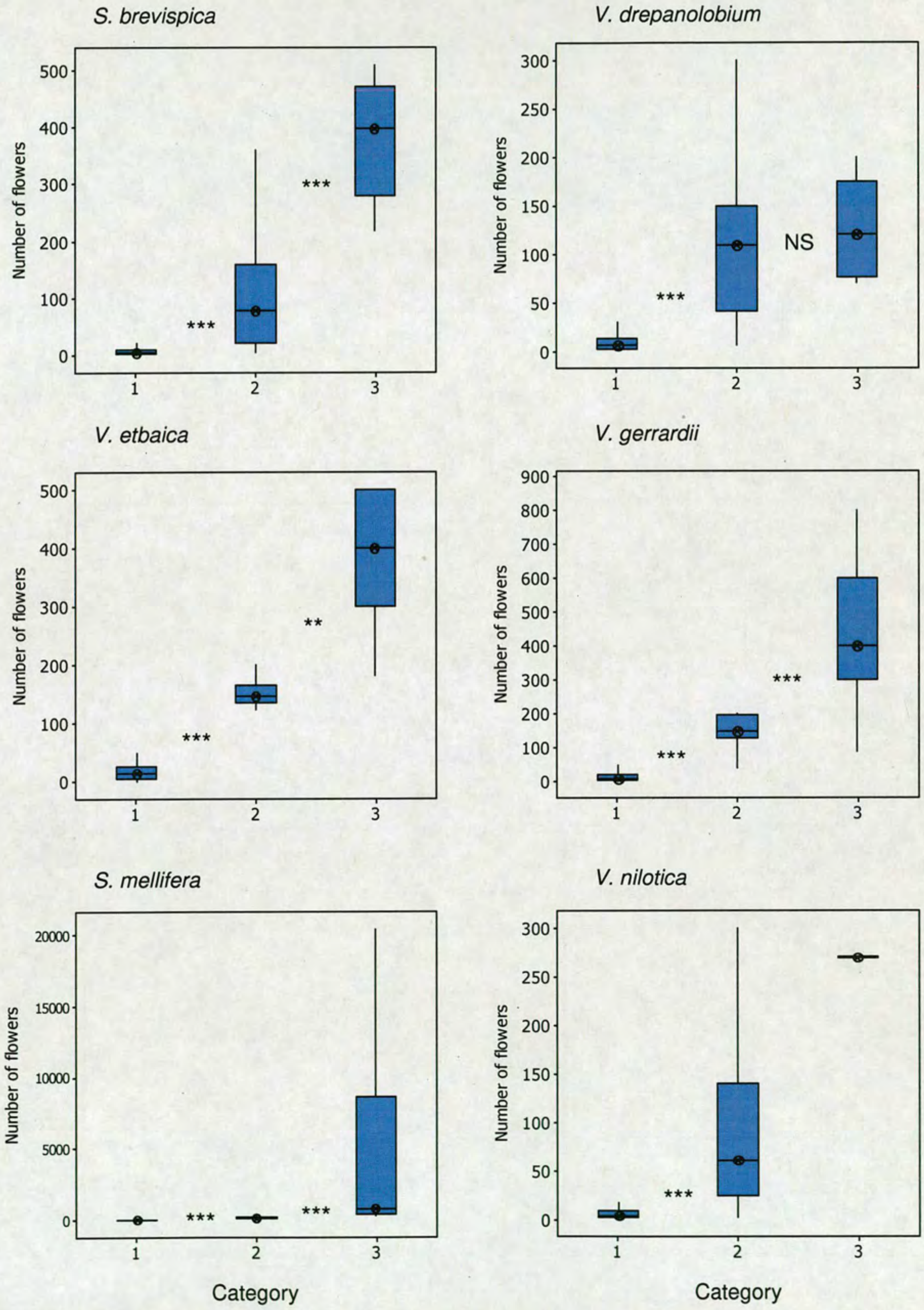


Figure 3.5 Median values (circles) and interquartile ranges (blue boxes) for quantitative count data across all sites corresponding to the categories used to score flower presence in the long term phenology dataset. Asterices indicate the results of Mann Whitney tests used to compare the median values of each category.

## 3.4 Discussion

### 3.4.1 Flowering phenologies of the Mpala acacias

The majority of acacia species at Mpala had bimodal flowering phenologies. *Senegalia brevispica* had a trimodal flowering phenology. For most species these patterns were repeated across sites and across years. Although flowering peaks occurred at specific times for each species, in several species (*S. brevispica*, *V. drepanolobium*, *V. gerrardii* and *V. nilotica*) some flowering occurred during most months of the year.

Although there was some variation between sites and years, the flowering phenologies of each species can be characterised as follows:

- *Senegalia brevispica* had a trimodal flowering pattern at all sites (Fig. 3.3). The three peaks of flowering generally corresponded to the three annual rainfall peaks (Table 3.3, Fig. 3.4).
- *Vachellia drepanolobium* flowered during most months of the year but flowering was lowest in July and August (Fig. 3.1). This species had a bimodal flowering pattern at all sites. Flowering peaks occurred in approximately April-May and October-November and flowering intensity was similar for both peaks.
- *Vachellia etbaica* had an overall bimodal flowering pattern although flowering did not occur twice each year at all sites (Fig. 3.1, Appendix 2). Trees at MRC and Turkana Boma had a stronger flowering peak between late July and late September and a smaller peak in February and March (Fig. 3.2). At Mukenya trees flowered at approximately the same times but flowering intensity was greater and flowering seasons were longer (Fig. 3.2). *Vachellia etbaica* trees at Junction had extremely low levels of flowering (Fig. 3.2).
- *Vachellia gerrardii* had a bimodal flowering pattern with peaks occurring in approximately March-May (incorporating the long rains) and July-November (incorporating the July/August rains and short rains) (Figs. 3.1, 3.2). Flowering occurred during most months of the year but tended to be lower in December-January and June-July (Figs. 3.1, 3.2).
- *Vachellia hockii* flowered at lower intensities than most other species. The overall pattern across years suggested a bimodal flowering pattern, although flowering

did not occur in sampled trees during every year of the study (Fig. 3.1, Appendix 2).

- *Senegalia mellifera* had a bimodal flowering pattern with flowering occurring in approximately March-April and late October-November (Fig. 3.1). At Mukenya and Turkana Boma flowering also occurred in September (Fig. 3.2).
- *Vachellia nilotica* flowering was bimodal with peaks in February-March and July (Fig. 3.1). Trees of this species flowered during most months of the year although flowering was lowest in April-May and December-January.
- *Vachellia seyal* flowered at lower intensities than many other species (Fig. 3.1). The modality of flowering was not clear as the number of peaks varied between years at both sites at which this species was present (Appendix 2).
- *Vachellia tortilis* had an overall bimodal flowering phenology although did not flower during all study years (Fig. 3.1, Appendix 1). Flowering peaks occurred in approximately February-March and August-October. Flowering intensity was lower than in most other species, although larger flowering peaks occasionally occurred.
- *Vachellia xanthophloea* had an overall bimodal flowering phenology although did not flower during all study years (Fig. 3.1, Appendix 1). Flowering occurred in February-March and in August-November. Trees of this species flowered at relatively low intensities.

### 3.4.2 Co-flowering among the Mpala acacias and implications for competition for pollination

There is no strong evidence for highly structured multi-species co-flowering among the acacias at Mpala. Regular co-flowering among large groups of acacia species was rare and several species were able to flower during most months of the year. Co-flowering occurred predominantly between groups of two, three or four species although even the species that co-flowered most often with other acacias (*S. brevispica*, *V. drepanolobium*, *V. gerrardii*, *V. nilotica* and *V. seyal*) co-flowered with different species across sites and years. Despite a large number of acacia species having bimodal flowering patterns, flowering peaks of different species did not necessarily occur together.

Although flowering for the majority of species was not highly structured in seasonal time, co-flowering between acacia species was common. *Senegalia brevispica*, *V. drepanolobium*, *V. gerrardii, V. nilotica* and *V. seyal* flowered most frequently at all sites at which they were present, and all except *V. seyal* were widespread at Mpala. Since these species frequently co-flowered with one another, they might employ alternative strategies to minimise competition for pollination if key pollinator species are shared.

Stone et al. (1996, 1998) found that visitor assemblages differed between Tanzanian acacia species that offered both pollen and nectar as rewards to flower visitors and those that offered only nectar, although all species were visited by megachilid bees and calliphorid flies. They also demonstrated that the maximum pollen availabilities for a group of co-flowering acacias were significantly regularly spaced in daily time, resulting in the partitioning of shared pollinator visits in daily time. Consequently, we might expect a similar mechanism to exist among co-flowering acacias at Mpala that share pollinators. To investigate this possibility, in Chapter 4 I examine the daily patterns of pollen availability for co-flowering acacia species at Mpala for evidence of divergence in the timing of dehiscence among species in daily time, and in Chapter 5 I examine the visitor assemblages and daily patterns of flower visitation for co-flowering acacia species for evidence of the partitioning of shared visitors in daily time.

### 3.4.3 Comparisons with other studies of acacia flowering phenologies

*(a) African and Mexican acacias (genera* Vachellia *and* Senegalia*)*

Three previous studies have investigated the flowering phenologies of multiple sympatric acacia species in Africa, two in Tanzania (Stone et al. 1998, Mduma et al. 2007) and the other in South Africa (Milton 1987). Co-flowering regularly occurred among groups of acacia species in all three studies. The flowering phenologies of the species in these studies that were also found at Mpala are described in Table 3.7.

In a study of ten acacia species at Mkomazi in northern Tanzania, Stone et al. (1998) found that eight species flowered in December and January after the main autumn rains, with the main flowering peak for five species occurring during these months (Table 3.6). Several species flowered between May and July after the less intense Eastern rains, although only *S. brevispica* flowered predominantly at that time, whilst a minority of species flowered during the dry season (Table 3.6). Species at this site flowered at specific times and species' flowering peaks often occurred simultaneously. This contrasts with the flowering phenologies of the Mpala acacias, many of which flowered for longer periods and whose flowering peaks rarely coincided with those of multiple other species.

Table 3.6 Seasonal flowering patterns of Mkomazi acacia species. An "m" indicates mass flowering, and an "s" indicated slight, scattered flowering. Reproduced from Stone et al. (1998).

| | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Eastern rains | | | | | | | | | | | | |
| *S. brevispica* | s | | | | m | m | s | | | | | s |
| Summer dry season | | | | | | | | | | | | |
| *S. bussei* | | | | | | | | | s | m | m | s |
| *V. etbaica* | | | | | | | | s | m | m | | |
| *V. reficiens* | s | | | | | | | s | m | m | s | s |
| *S. thomasii* | | | | | | | m | m | s | | s | |
| Autumn rains | | | | | | | | | | | | |
| *V. drepanolobium* | m | s | | | s | s | s | | | | | m |
| *V. nilotica* | m | s | | | | s | s | | | | | m |
| *S. senegal* | m | s | | | | s | s | | | | s | m |
| *V. tortilis* | m | s | | | | | s | s | | | | m |
| *V. zanzibarica* | m | | | | | s | s | | | | s | m |

Mduma et al. (2007) examined flowering phenologies for nine acacia species at five sites in the Serengeti, Tanzania. Rainfall at this location is bimodal with long rains during March-May and short rains during November-December. Eight species had bimodal flowering patterns, and the other had a single annual flowering peak (Table 3.7). All species had flowering peaks after the short rains, between January and March. Bimodal species had a second flowering peak in approximately July-September. Data presented were summaries of species across sites therefore it is difficult to determine whether species co-flowered, but the similarities in seasonal flowering patterns indicate that there was the potential for co-flowering among the acacias at this location.

Table 3.7 Patterns of flowering in Tanzania (Stone et al. 1998, Mduma et al. 2007) and South Africa (Milton 1987) for acacia species found at Mpala

| | Stone et al. (1998), Mkomazi, Tanzania | | Mduma et al. (2007), Serengeti, Tanzania | | Milton (1987), South Africa |
|---|---|---|---|---|---|
| | Flowering pattern | Co-flowering species | Flowering pattern | Simultaneously flowering species | Flowering pattern and co-flowering species |
| *S. brevispica* | Bimodal with a stronger peak in May-June (after Eastern rains) and a smaller peak in December-January (after main rains) | Flowering occurs with other acacias but the main flowering peak does not overlap with that of any other species | - | - | - |
| *V. drepanolobium* | Bimodal with a stronger peak in December-February (after main rains) and a smaller peak in May-July (after Eastern rains) | Main flowering peak coincides with that of four other acacias and scattered flowering in three species | Bimodal with a stronger peak in January and a smaller peak in September | Main flowering peak coincides with peaks for eight other acacias | - |
| *V. etbaica* | A single peak in the dry season between August and October | Main flowering peak coincides with that of two other species | - | - | - |
| *V. gerrardii* | - | - | Bimodal with a stronger peak in January and a smaller peak in August | Main flowering peak coincides with peaks for four other acacias | - |
| *S. mellifera* | - | - | Bimodal with a stronger peak in January and a smaller peak in August | Main flowering peak coincides with peaks for four other acacias | Flowers once a year with two *Senegalia* species at end of dry season/start of rainy season. |
| *V. nilotica* | Bimodal with a stronger peak in December-February (after main rains) and a smaller peak in June-July (after Eastern rains). | Main flowering peak coincides with that of four acacias and scattered flowering in three species | - | - | Flowers once a year with three *Vachellia* species during the rainy season. |
| *V. seyal* | - | - | Bimodal with peaks in February and September | Flowering peaks correspond with peaks for four other acacias | - |
| *V. tortilis* | Bimodal with a stronger peak in December-February (after main rains) and a smaller peak in July-August (after Eastern rains). | Main flowering peak coincides with that of for four acacias and scattered flowering in three species | Bimodal with peaks in February and August | Flowering peaks correspond with peaks for four other acacias | Flowers once a year with three *Vachellia* species during the rainy season. |
| *V. xanthophloea* | - | - | Bimodal with a peak in August and a lower peak in March | Flowering peaks correspond with peaks for three other acacias | - |

Milton (1987) examined the flowering phenologies of seven sympatric acacia species in South Africa. All species flowered once a year with species co-flowering during two distinct periods. Species in different genera flowered at different times with three *Senegalia* species flowering between August and October and four *Vachellia* species flowering between December and February. Rainfall at the study site was unimodal with rains lasting from approximately October until April.

Raine (2001) examined the flowering phenologies of four acacia species (three *Vachellia* and one *Senegalia* species) in dry seasonal forest in Mexico. Species flowered in synchrony with the onset of predictable rain and species frequently co-flowered for extended periods, although peaks in flowering effort divided the acacia community into two species pairs that peaked either at the end of the dry season (*V. farnesiana* and *V. hindsii*) or at the start of the wet season (*S. angustissima* and *V. macracantha*). *Vachellia farnesiana* and *V. hindsii* received visits from different potential pollinators, whereas *S. angustissima* and *V. macracantha* had similar visitor assemblages. In locations where these species co-flowered, *S. angustissima* and *V. macracantha* appeared to partition pollinator visits in daily time through differing patterns of pollen availability.

### *(b) Australian acacia flowering phenologies (genus* Acacia*)*

In Australia, acacias are able to flower in all months of the year (Maslin 2001) but individual species usually flower at a particular seasonal time (Davies 1976, Prescott 2005). Acacias in arid zones often have different flowering patterns to those in temperate regions (Friedel et al. 1994). In Western Australia Davies (1976) found that arid-zone acacia species flowered throughout the year, although each species flowered at a specific time, with different sets of between two and four acacia species co-flowering in autumn, winter, early summer and late summer.

The majority of acacia species in Victoria, in temperate south-eastern Australia, flower during the transition from the cool, wet winter into the mild, wet spring, although individual species' distributions will determine the extent to which co-flowering actually occurs among species (Prescott 2005). Prescott (2005) also examined flowering patterns for a community of seven sympatric acacias near Melbourne, Victoria, and found that flowering peaks of individual species were significantly regularly spaced between July and October (late winter-early spring) although flowering did overlap between species. Average rainfall for the region is highest during these months. Since the acacias at this site offered the same rewards and shared pollinators, Prescott (2005) suggests that the structuring of flowering in seasonal time at this site could be driven by competition for shared pollinators resulting in the divergence of flowering between species in seasonal time.

*(c) Flowering phenologies of taxa related to acacias*

Koptur (1983) examined the flowering phenologies for a group of *Inga* species in Costa Rican cloud forest. The genus *Inga* belongs to the tribe Ingaeae, previously a sister tribe to Acacieae, although recent phylogenetic studies (see Section 2.2.3) suggest that the Australian acacias are more closely related to species in this tribe than to African and neotropical acacias in the genera *Vachellia, Senegalia, Mariosousa* and *Acaciella*. Like acacias, the *Inga* species in this study all had flowers that were similar in structure and appearance. All species studied produced nectar that was accessible to a wide range of visitors, and pollinators were shared between species. Despite variation between flowering phenologies, flowering seasons overlapped substantially for a number of *Inga* species with several species flowering at the wet/dry season interface. Differences in floral behaviour, in terms of flower opening times and patterns of flower opening, helped to some extent to partition pollinator visits in daily time among co-flowering species, and may have reduced the negative consequences of pollinator sharing. This is the same resource axis along which some co-flowering acacia communities might diverge in response to competition for pollinators (Stone et al. 1996, 1998, Raine 2001).

*Mimosa* species (tribe Mimoseae) have a similar floral structure to acacia flower heads, and have been grouped with acacias at various points in their taxonomic history. Camargo-Ricalde et al. (2004) examined the flowering phenologies for seven endemic *Mimosa* species in Mexico. All species flowered during the rainy season (April-September) and flowering continued into the dry season for some species. Since species varied in their geographical locations, co-flowering among *Mimosa* species would depend on the distribution of individual species.

### 3.4.4 Rainfall as a causal factor of acacia flowering phenologies at Mpala

In seasonal habitats with marked wet and dry seasons, plant reproduction can be driven by water availability and species' flowering phenologies are often dictated by annual rains (Rathcke and Lacey 1985, van Schaik et al. 1993). In seasonal habitats in Tanzania (Stone et al. 1998, Mduma et al. 2007), South Africa (Milton 1987) and Mexico (Raine 2001) the flowering phenologies of acacias were found to be linked to patterns of rainfall. At Mkomazi in Tanzania, the majority of acacia species flowered after periods of rain with fewer species flowering during the dry season (Stone et al. 1998). In the Serengeti flowering patterns were shown to be highly correlated with rainfall (Mduma et al. 2007). In South Africa one group of acacias flowered at the start of the annual wet season and another during the rains (Milton 1987). In Mexico all acacia species studied flowered during the annual rains between June and October (Raine 2001). In contrast, acacia species in Australia are able to flower throughout the year (Davies 1976, Prescott 2005) and species flowering in temperate regions that are not constrained by seasonal rainfall may have diverged in their seasonal flowering peaks to avoid competition for shared pollinators (Prescott 2005).

As at the Tanzanian study sites, the habitat at Mpala is seasonal, with pronounced wet and dry seasons. Rainfall occurs in approximately March-April and November-December, as it does in most parts of East Africa (see McWilliam and Packer 1999). Therefore we might expect acacia flowering phenologies at Mpala to be linked to this rainfall pattern. Indeed, many species do show a bimodal flowering pattern; however there is no clear association between acacia flowering patterns and rainfall, and species' flowering peaks do not coincide after the rains as they do at Mkomazi. In addition to the usual two sets of rains, the region in which Mpala is located receives an additional period of rain during August resulting in a trimodal pattern of rainfall (Fig. 3.2). This results in a wetter climate during what is usually a long dry season in many other areas. It is possible that this additional period of rain has influenced the flowering phenologies of the acacia species in this region. For example, *V. drepanolobium* and *V. nilotica*, which flower after the rains at Mkomazi, flower for longer periods at Mpala (Tables 3.3, 3.6). Furthermore, *S. brevispica* flowers after both sets of rains and is bimodal at Mkomazi whilst at Mpala its flowering phenology closely tracks the trimodal rainfall, with flowering occurring soon after each period of rain (Tables 3.3, 3.6).

One hypothesis for the trimodality seen in *S. brevispica* is that this species alone has been able to adapt to the trimodal rather than bimodal rainfall pattern evident at Mpala. This begs the question of why the other species (if the pattern in *S. brevispica* is adaptive) have failed to do so. *Senegalia brevispica* is a short-lived 'weedy' acacia species and its generation time is likely to be substantially shorter than for the longer lived woody species (Dharani 2006). This in turn (all other things being equal) predicts a greater rate of adaptive change in *S. brevispica*. *Senegalia brevispica* is phylogenetically distinct both from the *Vachellia* acacias and from its congener, *S. mellifera* (Joe Miller, Iowa State University, Plant Genomics Laboratory, pers. comm.) and it is also possible that lineages other than *S. brevispica* have experienced greater phylogenetic constraint in adaptive response to rainfall patterns. This hypothesis, and the underlying assumption that flowering phenology shifts are indeed adaptive, could both be tested by examining broader geographic variation in the phenology of these different acacia groups. To date, no appropriate data for such a comparison exist.

### 3.4.5 Critique of methods

To my knowledge, the results in this chapter represent the longest running phenological dataset anywhere in Africa. Furthermore, data were collected on a finer timescale than for any known acacia flowering phenology study. The aim of this study was to compare the flowering phenologies of the Mpala acacia species to enable the identification of regular co-flowering species assemblages. Data collection using a qualitative four-point scale was sufficient for this. Qualification of this scale using quantitative data revealed that categories on this scale represented significantly different numbers of flowers for most acacia species examined. Therefore our sampling method was effective for the majority of species at this location.

To further investigate the relative intensities of co-flowering species, the information on the absolute number of flower heads represented by each qualitative category gained from the quantitative studies could be incorporated into the comparisons of co-flowering species. This would reveal in more detail which species are co-flowering more intensely.

Determination of the causal mechanisms that drive species' flowering phenologies was beyond the scope of this study, although visual comparisons were made between flowering phenologies and rainfall patterns. Information on bud and fruit production collected at the same time as the flowering data presented in this chapter could provide further evidence regarding the structuring of acacia species flowering and fruiting times in relation to rainfall. Flowering phenologies could be dictated by optimal fruiting times for individual species (Primack 1987).

# Chapter 4. Daily patterns of pollen availability for the Mpala acacia species

## Summary

Co-flowering plant species that share pollinators could minimise competition for pollination by diverging along alternative resource axes. Previous work has shown that co-flowering acacia species in Tanzania and Mexico partition visits by shared pollinators in daily time through divergence in the timing of dehiscence.

To assess whether a similar mechanism occurs among the co-flowering acacias at Mpala, daily patterns of pollen release were examined for the ten species present: *S. brevispica*, *V. drepanolobium*, *V. etbaica*, *V. gerrardii*, *V. hockii*, *S. mellifera*, *V. nilotica*, *V. seyal*, *V. tortilis* and *V. xanthophloea*. Competitive displacement predicts intraspecific synchrony and regular spacing between species.

The Mpala acacias dehisced during the day, between 9.00 (*V. xanthophloea*) and 15.00 (*S. brevispica*). Although the acacias form a dehiscence sequence through the day, low intraspecific synchrony and high interspecific overlap provide little evidence to support the role of competitive displacement in dehiscence times in this community.

It is thus unlikely that pollinator visits are partitioned in daily time through bottom-up patterning in floral resources.

The findings of this study contrast with those of Stone et al. (1996, 1998) who found significant regular spacing in the timing of dehiscence among co-flowering acacia assemblage in Tanzania. Contrasts between these results and those of this thesis are discussed.

## 4.1 Introduction

In Chapter 3, I established which acacia species most often co-flowered at Mpala to identify which sets of species might compete for pollination. In this chapter I examine the daily patterns of pollen availability for the Mpala acacias and use this to determine whether co-flowering acacia species structure pollen availability in daily time. If pollen availability peaks for co-flowering species are regularly spaced in daily time, and shared pollinators track pollen availability, this could be evidence for daily temporal partitioning of pollinators through divergence in the timing of dehiscence, due to competition for pollination.

### 4.1.1 Resource partitioning as a mechanism for avoiding competition for pollination

Competition for pollinators between sympatric plant species can be reduced through the segregation of flowering periods (Levin and Anderson 1970, Mosquin 1971, Heithaus 1974, Stiles 1977, Waser 1978a, Pleasants 1980, Kephart 1983, Rathcke 1983, Aizen and Vazquez 2006). However, in highly seasonal habitats plants tend to flower together during certain short periods throughout the year when conditions are more favourable for flowering (Janzen 1967b, Johnson 1992), hence restricting the potential for competition avoidance through separation in seasonal time. Plant species constrained to flower simultaneously could reduce competition for shared pollinators by structuring the daily timing of visits to flowers (Levin and Anderson 1970, Koptur 1983). This can be achieved through the separation of the presentation of floral resources in daily time. As described in Chapter 1, this was first detailed in *Dalechampia* vines (Armbruster and Herzig 1984).

### 4.1.2 Evidence for daily temporal resource partitioning in acacias and related species

Stone et al. (1996, 1998) presented evidence for the partitioning of pollinators in daily time among six co-flowering acacia species in Tanzania. Peaks of pollen availability for the six species were significantly regularly spaced throughout the day, a pattern which is compatible with competitive displacement. Patterns of visitation by shared pollinators closely tracked pollen availability in each species.

This study demonstrated that the partitioning of pollinators in daily time can occur among large groups of co-flowering species.

This mechanism could be particularly important for acacias since their stigma structure usually allows only one polyad to occupy the receptive surface (Kenrick 2003). Hence deposition of polyads from other acacia species could result in stigma blockage preventing any future successful pollination. Furthermore, both anthers and stigmas are presented on the surface of flower heads and polyads are easily deposited on the bodies of foraging visitors. Therefore visitors foraging indiscriminately among several acacia species are likely to transfer polyads between species.

Raine (2001) demonstrated that two co-flowering acacia species in Mexico differed in their daily timing of dehiscence, with one species dehiscing in the morning and the other in the afternoon. As in the Tanzanian study, shared pollinators visited the acacia species with the highest pollen availability, so that species were visited at different times. Evidence of pollinator partitioning has also been found for species closely related to acacias. Koptur (1983) showed that co-flowering *Inga* species in Costa Rica that shared pollinators differed in the daily timing of flower opening and presentation of floral resources. Like acacia flower heads, *Inga* flowers are open in structure and pollen is accessible to a wide variety of visitors.

### 4.1.3 The effect of relative humidity on the timing of dehiscence

The timing of anther dehiscence can be sensitive to a variety of microclimatic cues, particularly relative humidity (Buchman 1983, Corbet 1990). The timing of dehiscence in Tanzanian and Mexican acacias was found to be linked to relative humidity (Stone et al. 1998, Raine 2001) and these studies suggested that particular humidity levels acted as a cue for dehiscence in some species. Furthermore different species dehisced at different relative humidities. This suggests that even if relative humidity and the rate at which it chaged varied between days, the acacias would still dehisce in the same order, maintaining the sequence of pollen availability among species. The examination of dehiscence times within species should therefore incorporate variation in relative humidity in order to establish whether observed variation in the timing of dehiscence could be due to microclimatic variation between days, or is attributable to a lack of synchrony within a species.

### 4.1.4 Examination of pollen availability patterns in daily time for the Mpala acacia species

Given the evidence for pollinator partitioning in daily time in acacias, it is possible that the co-flowering acacia species at Mpala have evolved similar structuring to reduce competition for pollination. Character displacement due to competition predicts both intraspecific synchrony and interspecific divergence (see Chapter 1). To determine whether this is the case at Mpala, we need to demonstrate (i) intraspecific synchrony in dehiscence, (ii) divergence in timing of dehiscence across species in a pattern predicted for competitive displacement and (iii) tracking of pollen release across acacia species by shared pollinators. In this chapter I examine the daily patterns of dehiscence and pollen availability for the Mpala acacias using methods similar to those used in previous studies (see Section 4.2.2), and in Chapter 5, I examine the floral visitor assemblages and daily patterns of visitation for each acacia species.

In this chapter I address the following specific questions:

1. Do the Mpala acacia species show intraspecific synchrony in their daily patterns of pollen availability? How do these patterns vary:
    (a) across individuals on a given day,
    (b) for an individual across days,
    (c) amongst species within and between sites?

2. Can variation in the timing of dehiscence within species be explained by variation in relative humidity?

3. Do differences in the daily timing of dehiscence between species provide evidence of competitive displacement?

## 4.2 Methods

### 4.2.1 Study sites

Daily patterns of pollen availability were examined between 1998 and 2005 for acacia trees at the eight sampling sites used for the collection of long term flowering phenology data in Chapter 3. Further information regarding the acacia species assemblages at these sites can be found in Chapter 2. Data from 1998-2003 were collected by Dr G. N. Stone, Professor P. G. Willmer, Dr R. Atkinson, S. Whiten, Professor A. Schnabel, Dr J. A. Rowe and R. Eraguy. Data from 2003 to 2005 were collected by myself, Dr G. N. Stone and R. Eraguy.

Data were collected for a total of 178 tree days across all sites (Table 4.1), more than twice the number in Stone et al.'s (1998) study of Tanzanian acacias (74 days). The sampling dates and number of trees sampled on each day are shown in Table 4.1. Where flowering allowed, I sampled all acacia species at each site.

### 4.2.2 Determining patterns of pollen availability through time

On most days sampling was carried out between 6.00 and 17.00. Dawn occurred shortly before 6.00 and dusk at approximately 18.00. No acacia species dehisced during the night. On some days data collection started later or finished earlier due to weather constraints, difficulties with field access, or the proximity of wild animals preventing access to sampling trees. Where possible, on each sampling day at each site a minimum of three trees was sampled. The same marked individuals were sampled across days and across years wherever possible, in order to examine variation within individual trees.

The timing of dehiscence was estimated for each acacia species by examining the relative abundance of pollen available on the surface of flower heads sampled at intervals throughout the day using the methods developed by Stone et al. (1998). Most trees were sampled once per hour, although some trees in 1998 and 1999 were sampled at intervals of between 1.5 and 2 hours. At each sample time four flower heads were chosen at random from the tree with respect to aspect and height above ground. If too few flower heads were present on a tree for four to be sampled at every sample time throughout the day, only two were sampled per hour. Each flower

Table 4.1 Sampling effort for pollen availability data collected for each acacia species at each study site

| Acacia species | Site | Pollen sampling effort in tree days | Date |
|---|---|---|---|
| *S. brevispica* | MRC | 4 | 29th Jan 2001 |
| | MRC | 4 | 10th Dec 2003 |
| | MRC | 2 | 28th May 2005 |
| | MRC | 2 | 31st May 2005 |
| | MRC | 2 | 10th June 2005 |
| | Turkana Boma | 2 | 4th May 1998 |
| | Turkana Boma | 2 | 13th May 2003 |
| | Turkana Boma | 5 | 23rd Sep 2003 |
| | Turkana Boma | 2 | 20th Aug 2004 |
| | Junction | 2 | 5th June 2003 |
| | High Dam | 2 | 9th June 1999 |
| | High Dam | 3 | 17th June 1999 |
| | Boma | 5 | 27th Sep 2003 |
| **Total** | | **37** | |
| *V. drepanolobium* | Turkana Boma | 3 | 4th May 1998 |
| | Turkana Boma | 1 | 23rd Sep 2003 |
| | Turkana Boma | 2 | 7th Nov 2003 |
| | Turkana Boma | 2 | 6th Sep 2004 |
| | Turkana Boma | 1 | 13th Sep 2004 |
| | Junction | 1 | 30th July 2004 |
| | Junction | 3 | 10th Sep 2004 |
| | Junction | 2 | 17th Sep 2004 |
| **Total** | | **15** | |
| *V. etbaica* | MRC | 2 | 7th May 1998 |
| | MRC | 5 | 24th July 2001 |
| | MRC | 1 | 11th Aug 2003 |
| | MRC | 2 | 13th Aug 2003 |
| | MRC | 4 | 2nd Aug 2004 |
| | MRC | 4 | 7th Aug 2004 |
| | Turkana Boma | 2 | 4th May 1998 |
| | Turkana Boma | 2 | 23rd Sep 2003 |
| | Turkana Boma | 1 | 13th March 2004 |
| | Turkana Boma | 4 | 21st Aug 2004 |
| | Turkana Boma | 2 | 13th Sep 2004 |
| | Mukenya | 3 | 30th Aug 2002 |
| **Total** | | **27** | |
| *V. seyal* | Turkana Boma | 3 | 17th Sep 2001 |
| | Turkana Boma | 3 | 3rd Sep 2002 |
| **Total** | | **6** | |
| *V. hockii* | High Dam | **1*** | 17th June 1999 |

Table 4.1 (cont.) Sampling effort for pollen availability data collected for each acacia species at each study site

| Acacia species | Site | Pollen sampling effort in tree days | Date |
|---|---|---|---|
| *A. gerrardii* | Turkana Boma | 2 | 21st June 1999 |
| | Mongoose | 1 | 6th June 1999 |
| | Mongoose | 2 | 12th June 1999 |
| | Junction | 2 | 5th June 2003 |
| | Junction | 3 | 18th March 2004 |
| | Junction | 3 | 30th July 2004 |
| | High Dam | 2 | 16th June 1999 |
| | High Dam | 4 | 17th June 1999 |
| | High Dam | 3 | 28th July 2004 |
| **Total** | | **22** | |
| *S. mellifera* | MRC | 3 | 27th March 2004 |
| | MRC | 3 | 16th Feb 2005 |
| | Turkana Boma | 1 | 4th May 1998 |
| | Turkana Boma | 2 | 7th Nov 2003 |
| | Turkana Boma | 4 | 16th March 2005 |
| | Turkana Boma | 4 | 18th March 2005 |
| | Mukenya | 3 | 29th Sep 2002 |
| **Total** | | **20** | |
| *V. nilotica* | MRC | 1 | 14th June 2003 |
| | MRC | 3 | 25th June 2004 |
| | MRC | 2 | 2nd July 2004 |
| | Turkana Boma | 4 | 4th May 1998 |
| | Turkana Boma | 1 | 14th June 2003 |
| | Turkana Boma | 1 | 16th June 2003 |
| | Turkana Boma | 3 | 19th June 2003 |
| | Turkana Boma | 5 | 21st June 2004 |
| | Turkana Boma | 5 | 22nd June 2004 |
| | Turkana Boma | 5 | 29th June 2004 |
| | Turkana Boma | 5 | 6th July 2004 |
| | Turkana Boma | 5 | 16th July 2004 |
| | Mukenya | 3 | 9th Jan 2003 |
| | Junction | 1 | 30th July 2004 |
| | Junction | 1 | 10th Sep 2004 |
| | Junction | 1 | 17th Sep 2004 |
| **Total** | | **46** | |
| *V. tortilis* | Boma | **2** | 25th March 2004 |
| *V. xanthophloea* | River | **2** | 20th Sep 2003 |

* *Vachellia hockii* was sampled across three trees due to low flower density per tree. The daily pattern of pollen release was generated for this population by averaging across all three individuals per sampling interval.

head was removed from the tree and rolled lightly across the adhesive side of a piece of clear adhesive tape. The tape was placed on a slide and later examined with a light microscope at x40 magnification. To ensure compatibility among samples, a consistent rolling pattern is necessary and little pressure must be applied to the adhesive tape to avoid squashing undehisced anthers to expose pollen that might be included when counted under a microscope.

Acacia pollen is presented in the form of compound aggregates of pollen grains called polyads (Kenrick and Knox 1982). 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 dehisce polyads were also collected with numbers increasing as dehiscence took place, and decreasing as they were removed by visitors.

For each flower head the ratio of anthers to polyads was recorded for five randomly chosen microscope fields, and the mean calculated. The mean ratio was then calculated across the sampled flower heads for each tree at each time interval. This is referred to as the 'pollen to anther ratio'. Standardising the range in pollen to anther ratios among trees was necessary in order for each tree to contribute equally to means calculated across trees, days or sites. Therefore pollen to anther ratios were constrained to vary between zero and one for each tree on a particular day by dividing them by the maximum value recorded at any time interval for the tree on that day.

### 4.2.3 An example pattern of daily pollen availability

An example of a potential daily pollen availability pattern for a tree sampled hourly between 6.00 and 18.00 is shown in Figure 4.1. The amount of pollen available on the surface of flower heads at each time interval depends on two processes: (i) anther dehiscence releasing pollen and (ii) pollen collection and removal by floral visitors. Dehiscence begins at approximately 7.00 for this tree. The pollen to anther ratio increases sharply between 8.00 and 9.00, with maximum pollen availability occurring at 10.00. Removal of pollen by visitors could be occurring during this time. After 10.00 the rate of pollen removal by floral visitors exceeds the rate of presentation of pollen by dehiscence and the ratio of polyads to anthers decreases. The 'sharpness' of the pollen availability peak will give an indication of how rapidly visitors are removing pollen; a sharp narrow peak suggests that visitors are removing pollen very soon after it is released, whereas a flatter, broader peak suggests that the response of visitors to pollen release is slower and takes place over a longer period of time.

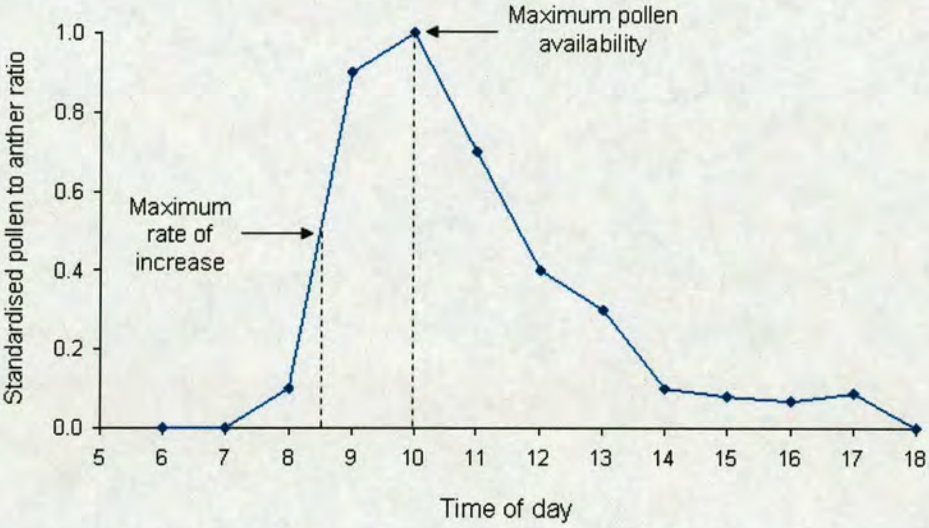


Figure 4.1 An example of a pollen availability curve, with hourly sampling between 6.00 and 18.00.

Two characteristics of the pollen availability curve can be used to estimate the timing of dehiscence: (i) maximum pollen availability, which is indicated by the highest pollen to anther ratio, and (ii) the maximum rate of increase in pollen availability, which is indicated by the largest positive slope between two consecutive sampling times (see Fig. 4.1). Previous studies of daily pollen availability patterns in acacias (Stone et al 1996, 1998, Raine 2001, Prescott 2005) have used the time at which the maximum amount of pollen is available to represent the timing of maximum dehiscence. Although the maximum rate of increase in pollen availability gives a better indication of the time when most pollen is released from anthers, pollinators are more likely to respond to the actual amount of pollen available on flower heads to time their visits (Roubik 1978, Buchmann and Cane 1989) which is best shown by considering the maximum amount of pollen available. Here I also use the time of daily maximum pollen availability to compare the timing of dehiscence between trees. Multi-peaked patterns of pollen availability meant that estimations of the maximum rate of increase for some of the trees in this study were problematic hence this was a less appropriate method for comparisons. Since it is possible that individual trees with maximum pollen availabilities occurring at the same time could commence dehiscence at different times, I also consider the general shape of daily pollen availability curves in comparisons.

### 4.2.4 Variation in pollen availability patterns within species

*(a) Variation across individuals on a given day*

Daily patterns of pollen availability for conspecific trees sampled on the same day were compared to examine the variation in dehiscence within a species on a single day. Williams' (1995) $V$ statistic was used to test for intraspecific synchrony in dehiscence by testing whether individual peaks of pollen availability were significantly aggregated between 6.00 (dawn) and 18.00 (dusk) (see Chapter 1, Section 1.4 for an explanation of how the $V$ statistic can be used to test for aggregation within daily time). The $V$ statistic could only be calculated for days on which three or more individuals were sampled. As multiple tests were carried out, the Bonferroni correction was applied. Twenty-seven tests were conducted requiring a significance level of $p=0.0019$ for rejection of the null hypothesis at an equivalent of $p=0.05$ for a single test.

*(b) Variation for an individual across days*

The daily patterns of pollen availability for individual trees sampled on two or more days were compared to examine the variation in timing of dehiscence for individual trees across days.

*(c) Variation across sampling days within sites*

The mean pollen availability at each time was calculated across all conspecific trees sampled on the same day to give an overall pattern of pollen availability for the species on that day. Means were constrained to vary between zero and one to allow comparisons. The mean patterns of pollen availability were compared between sampling days for each species at each site to examine the variation in timing of dehiscence within species populations. *Vachellia hockii, V. tortilis* and *V. xanthophloea* could not be compared across days since each was sampled on only one day.

*(d) Variation between sites*

The mean pollen availability at each time was then calculated across all days for each species at each site to give an overall pattern of pollen availability for the species at that site. Means were constrained to vary between zero and one to allow comparisons. The mean patterns of pollen availability for each species were compared between sites to examine the variation in timing of dehiscence across Mpala. *Vachellia hockii, V. seyal, V. tortilis* and *V. xanthophloea* could not be compared across sites since each was sampled at only one site.

### 4.2.5 Variation in pollen availability patterns between species

Williams' (1995) *V* statistic was used to examine whether the mean peaks of pollen availability for frequently co-flowering groups of acacia species were significantly regularly spaced in daily time. The species that co-flowered most frequently across years and across sites were *S. brevispica, V. drepanolobium, V. gerrardii, V. nilotica* and *V. seyal* (Chapter 3). The *V* statistic was calculated for combinations of these species for which pollen availability data were available (i) at each site, using the mean peaks of pollen availability for each species calculated across sampling days, and (ii) for the whole of Mpala, using mean peaks of pollen availability for each species calculated across sites. Calculation of the *V* statistic requires a minimum of three species, therefore species could not be compared at MRC, Mongoose, Mukenya, High Dam or Boma (Table 4.2).

The distribution of species' pollen availability peaks was examined within two ranges: (i) between dawn and dusk (6.00-18.00), (ii) between the first and last peak in the range. Examining the distribution between dawn and dusk is biologically justified since none of the Mpala acacias dehisced at night. Furthermore acacia species studied in Tanzania (Stone et al. 1996, 1998) dehisced between 6.00 and 15.00 and were visited by diurnal visitors. However, as the times between which acacias might be able to dehisce at Mpala are unknown, the distribution of species' peaks was also examined between the first and last peaks in the range (see Chapter 1, section 1.5 for an explanation of how the range used might affect the application of the *V* statistic). As multiple tests were carried out, the Bonferroni correction was applied. Seventy tests were conducted which meant that a threshold significance level of p=0.00071 was required for rejection of the null hypothesis at an equivalent to p=0.05 for a single test.

Table 4.2 Acacia species present at each site that regularly co-flowered across all sites and years. Pollen availability was sampled for only species in bold.

| Site | Sampled co-flowering species |
|---|---|
| MRC | ***S. brevispica, V. nilotica*** |
| Turkana Boma | ***S. brevispica, V. drepanolobium, V. gerrardii, V. nilotica, V. seyal*** |
| Mongoose | *S. brevispica, V. drepanolobium,* ***V. gerrardii*** |
| Mukenya | *S. brevispica, V. nilotica* |
| Junction | ***S. brevispica, V. drepanolobium, V. gerrardii, V. nilotica,*** *V. seyal* |
| High Dam | ***S. brevispica, V. gerrardii,*** *V. nilotica* |
| Boma | ***S. brevispica,*** *V. nilotica* |
| Overall | ***S. brevispica, V. drepanolobium, V. gerrardii, V. nilotica, V. seyal*** |

### 4.2.6 The effect of relative humidity on the timing of dehiscence

Relative humidity was recorded every hour or half hour using a Vaisala HMP31 humidity and temperature probe placed approximately 1 metre above the ground in the shade of one of the studied trees. Trees sampled on the same day were sited close to one another and data are assumed to be representative for all of the trees.

Data were available for the majority of trees sampled in 1998, 1999 and 2003-2005. Evidence for relationships between the time of maximum pollen availability and relative humidity were assessed using regression analyses conducted using Minitab 14.0. Previous studies (Stone et al. 1998, Raine 2001) have used the mean relative humidity over the two hours prior to dehiscence in analyses for each species. However in this study the timing of dehiscence was extremely variable for most species and therefore analyses were conducted using the mean relative humidity over several alternative two hour periods throughout the day. As multiple tests were carried out, the Bonferroni correction was applied. Thirty-nine tests were conducted which meant that a significance of p=0.0012 was required for rejection of the null hypothesis at an equivalent of p=0.05 for a single test.

## 4.3 Results

### 4.3.1 Do acacia species show intraspecific synchrony in the daily timing of pollen release?

Most acacia species at Mpala showed considerable variation in pollen availability patterns and the timing of dehiscence across individuals, days and sites. Table 4.3 shows the variation in the time of onset of dehiscence (the time at which the pollen to anther ratio started to increase) and maximum pollen availability across all individuals. Mean dehiscence times ranged from 9.00-15.00, and five species peaked on average at 10.00 (*V. drepanolobium*, *V. etbaica*, *V. gerrardii*, *V. hockii* and *V. seyal*). However, most species were extremely variable.

Table 4.3 Variation among individual sampling trees in the timing of onset of dehiscence and maximum pollen availability, and the time of mean maximum pollen availability calculated across all sampling days at each site, and then across all sites for each species.

| | Onset of dehiscence | Maximum pollen availability | |
|---|---|---|---|
| | | Range | Mean |
| *S. brevispica* | 6.00-12.00 | 8.00-17.00 | 15.00 |
| *V. drepanolobium* | 6.00-9.00 | 9.00-15.00 | 10.00 |
| *V. etbaica* | 6.00-11.00 | 6.00-15.00 | 10.00 |
| *V. gerrardii* | 7.00-11.00 | 8.00-15.00 | 10.00 |
| *V. hockii* | 8.30 | 10.00 | 10.00 |
| *S. mellifera* | 6.00-12.00 | 6.00-16.00 | 14.00 |
| *V. nilotica* | 6.00-12.00 | 6.00-17.00 | 12.00 |
| *V. seyal* | 6.00-8.00 | 8.00-13.00 | 10.00 |
| *V. tortilis* | 7.30 | 15.00-16.00 | 13.00 |
| *V. xanthophloea* | 6.00-8.00 | 9.00 | 9.00 |

*(a) Do trees sampled on the same day at the same site show synchrony in the timing of dehiscence?*

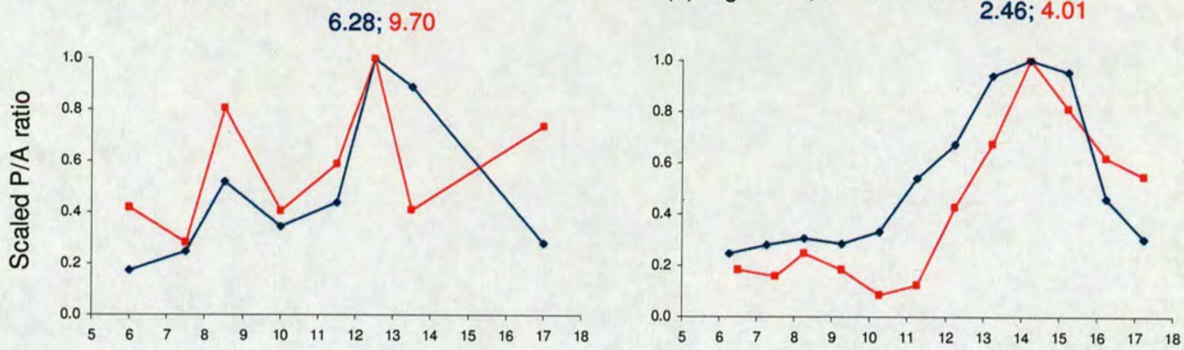
Individual trees sampled on the same day dehisced synchronously in *V. seyal*, *V. tortilis*, *V. xanthophloea*, and in *V. gerrardii* on most sampling days (Figs. 4.5, 4.8, 4.9). There was considerable variation amongst the *V. gerrardii* trees sampled on 30th July 2004 at Junction site (Fig. 4.5i). However, dehiscence may have been affected by the weather conditions on this day which were unusually cool with heavy rain after 15.00 that prevented further sampling. *Vachellia seyal* demonstrated synchrony in dehiscence on both days this species was sampled; however the maximum pollen to anther ratio for one of the trees sampled on 3rd September 2002 occurred much later in the day in comparison to the other two trees (Fig. 4.8).

*Senegalia brevispica*, *V. drepanolobium*, *V. etbaica*, *S. mellifera* and *V. nilotica* trees showed synchrony in dehiscence on some sampling days but in general these species showed more variation between trees (Figs. 4.2, 4.3, 4.4, 4.6, 4.7). The time of peak pollen availability was rarely consistent between trees sampled on the same day, even among individuals that began to dehisce at similar times (e.g. Figs. 4.4c, f, 4.6g). Several trees had multiple pollen availability peaks (e.g. Figs. 4.2d, 4.4d, 4.7g, k). For some individuals the pollen availability peak occurred at the beginning or end of a sampling day, occasionally accompanied by other smaller peaks during the day (e.g. Figs. 4.2h, i, 4.4e, h, 4.6e, g, 4.7g, k).

Calculation of the $V$ statistic on days on which three or more individuals of each species were sampled showed that peak pollen availabilities were not significantly aggregated in the period between dawn and dusk for any species at any site.

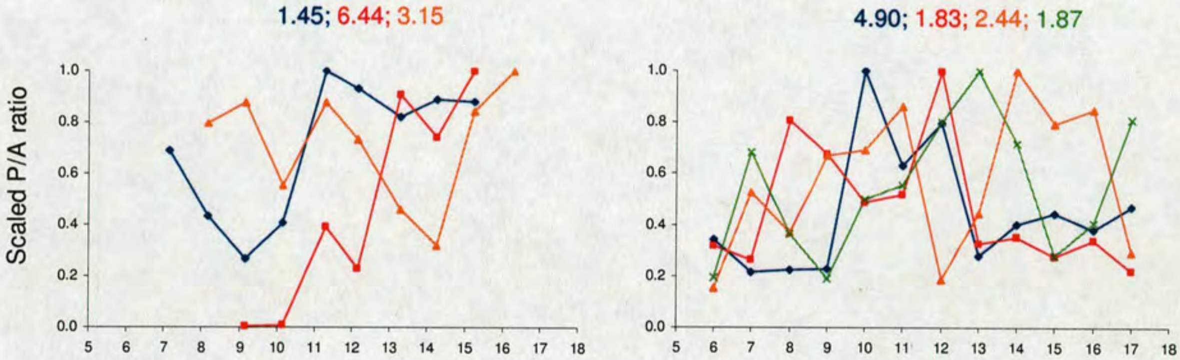
(a) Turkana Boma, 4th May 1998

(b) High Dam, 9th June 1999



(c) High Dam, 17th June 1999

(d) MRC, 29th Jan 2001



(e) Turkana Boma, 13th May 2003

(f) Junction, 5th June 2003

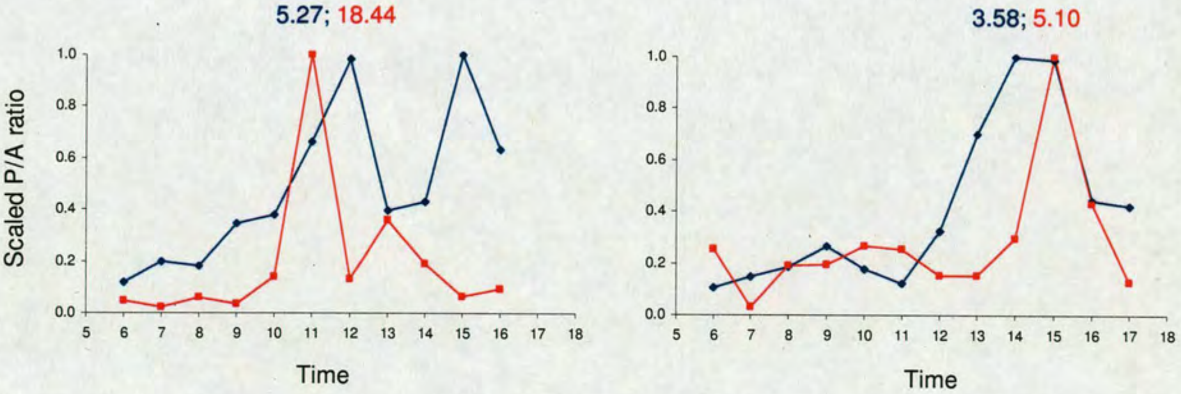
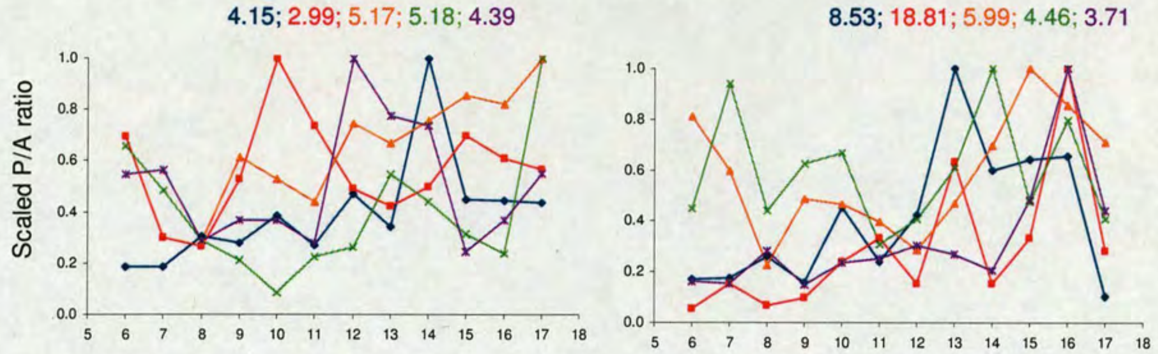
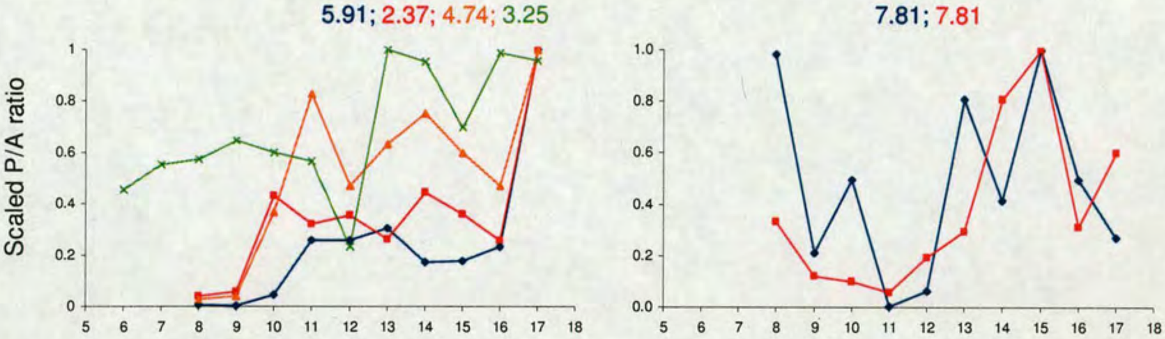


Figure 4.2 Daily patterns of pollen availability for individual trees of *S. brevispica* sampled on each day (a-m). The maximum absolute pollen to anther ratio for each tree is shown above the graph.



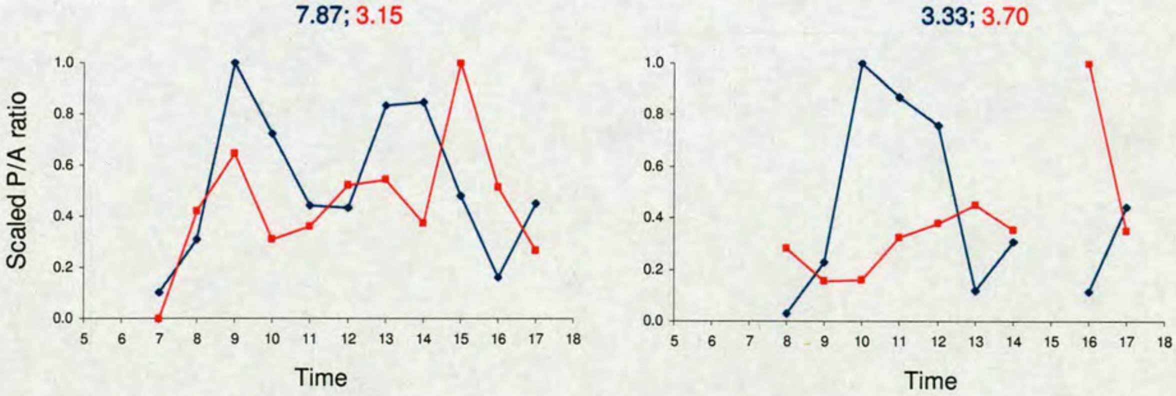
(g) Turkana Boma, 23rd Sep 2003

(h) Boma, 27th Sep 2003



(i) MRC, 10th Dec 2003

(j) Turkana Boma, 20th Aug 2004



(k) MRC, 28th May 2005

(l) MRC, 31st May 2005

(m) MRC, 10th June 2005

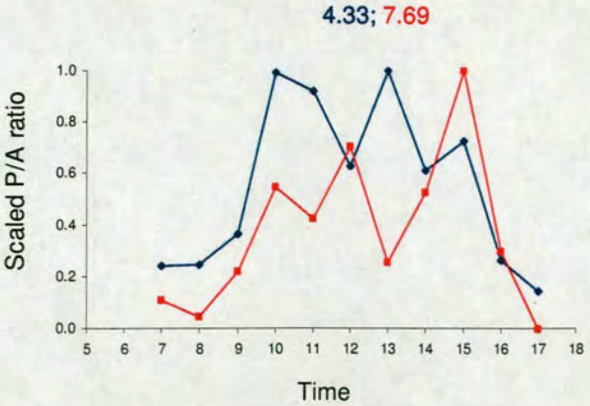
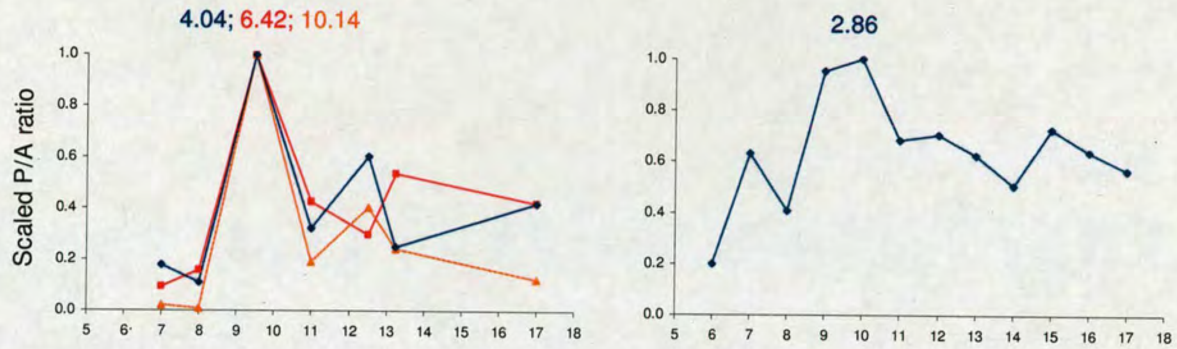
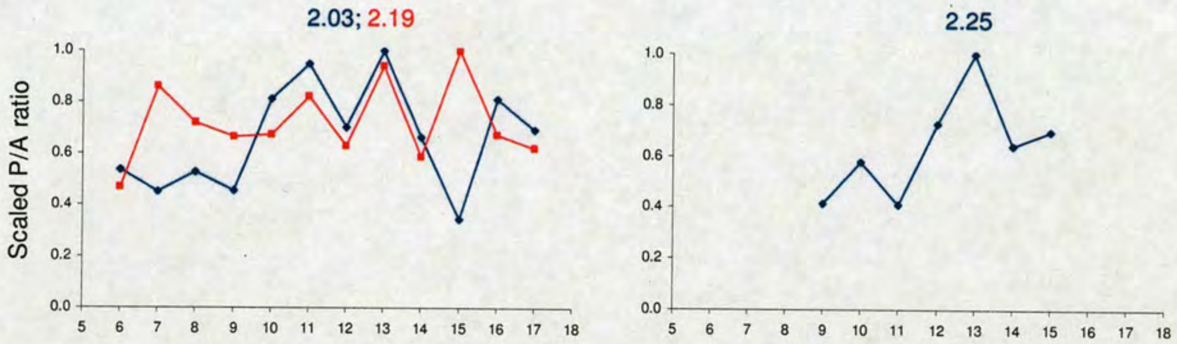


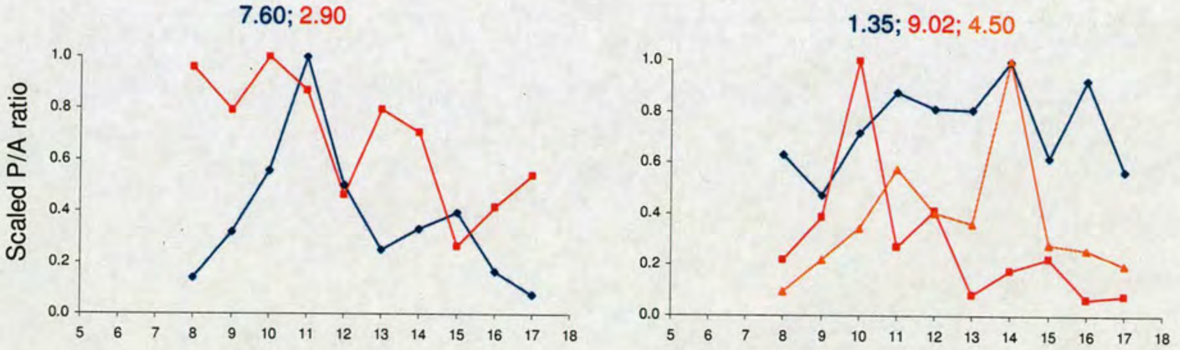
Figure 4.2 (cont.) Daily patterns of pollen availability for individual trees of *S. brevispica* sampled on each day (a-m). The maximum absolute pollen to anther ratio for each tree is shown above the graph.


(a) Turkana Boma, 4th May 1998

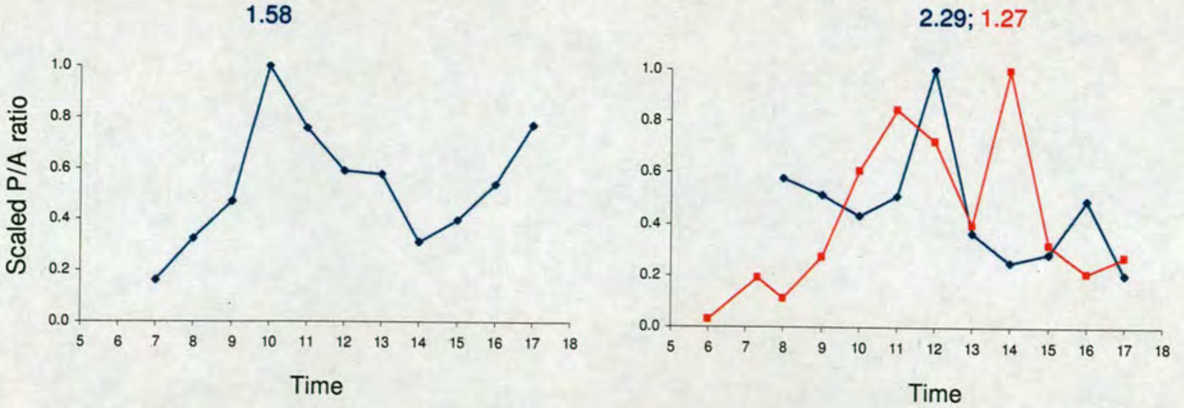
(b) Turkana Boma, 23rd Sep 2003


(c) Turkana Boma, 7th Nov 2003

(d) Junction, 30th July 2003

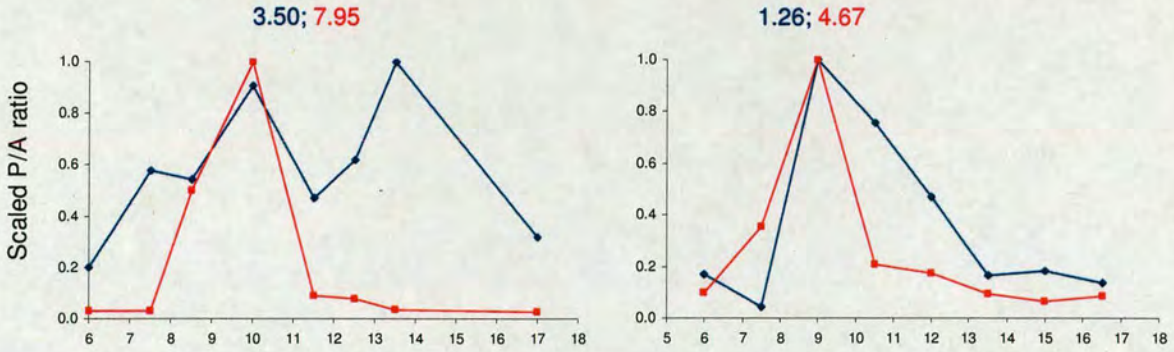

(e) Turkana Boma, 6th Sep 2004

(f) Junction, 10th Sep 2004

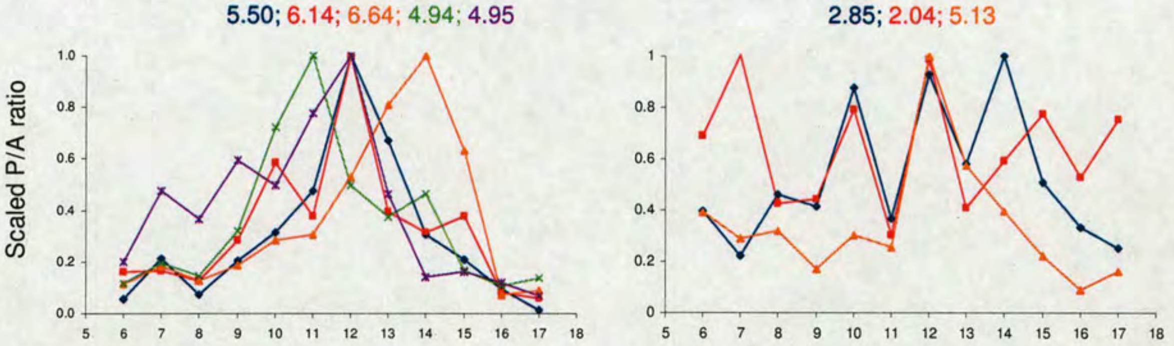

(g) Turkana Boma, 13th Sep 2004

(h) Junction, 17th Sep 2004

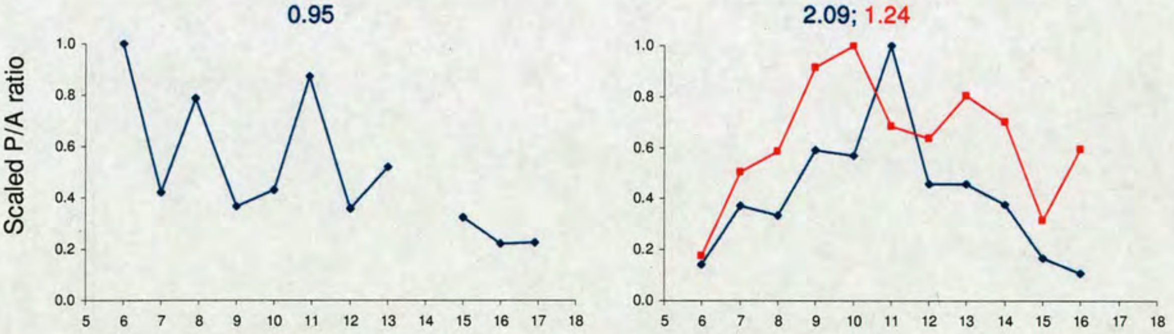
Figure 4.3 Figure 4.1 Daily patterns of pollen availability for individual trees of *V. drepanolobium* sampled on each day (a-h). The maximum absolute pollen to anther ratio for each tree is shown above the graph.


(a) Turkana Boma, 4th May 1998

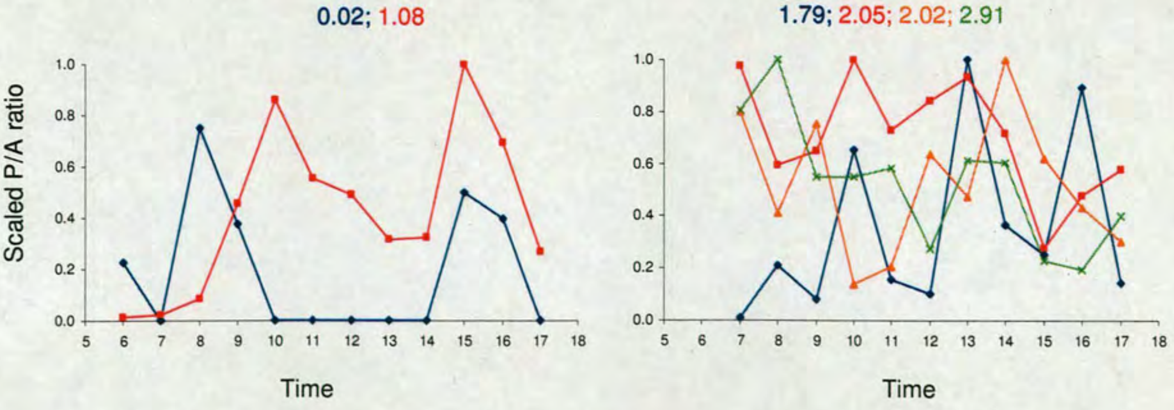
(b) MRC, 7th May 1998


(c) MRC, 24th July 2001

(d) Mukenya, 30th Aug 2002

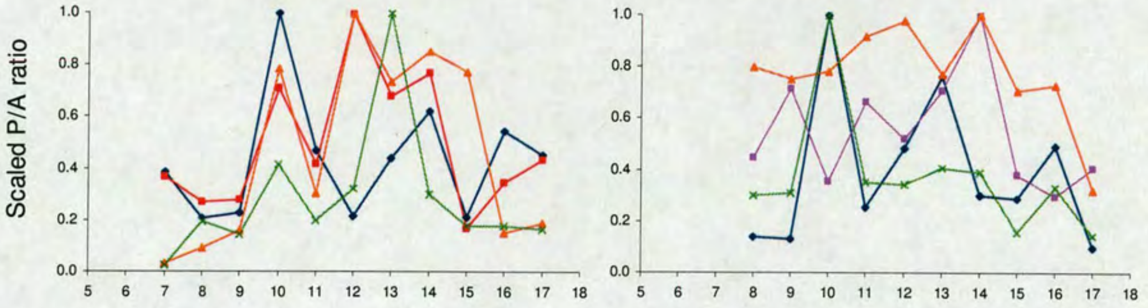

(e) MRC. 11th Aug 2003

(f) MRC. 13th Aug 2003


(g) Turkana Boma. 23rd Sep 2003

(h) MRC, 2nd Aug 2004

Figure 4.4 Daily patterns of pollen availability for individual trees of *V. etbaica* sampled on each day (a-l). The maximum absolute pollen to anther ratio for each tree is shown above the graph.

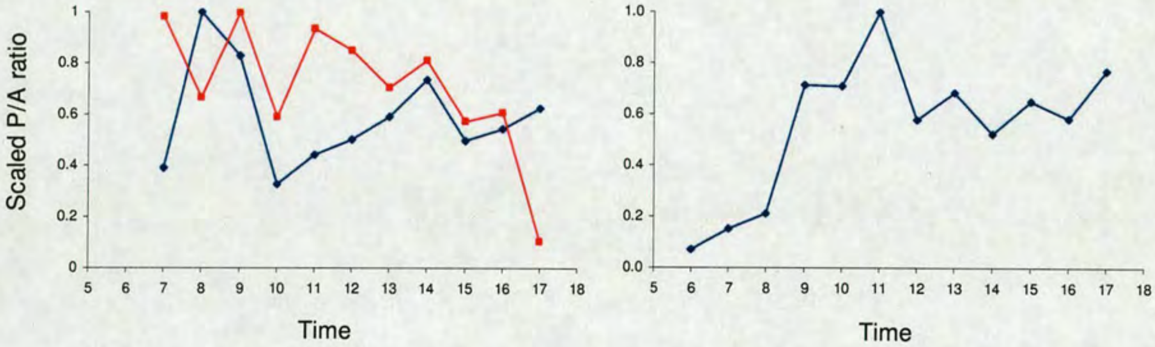


(i) MRC, 7th Aug 2004

2.46; 2.41; 3.16; 3.97

(j) Turkana Boma, 21st Aug 2004

2.56; 1.71; 1.39; 2.78



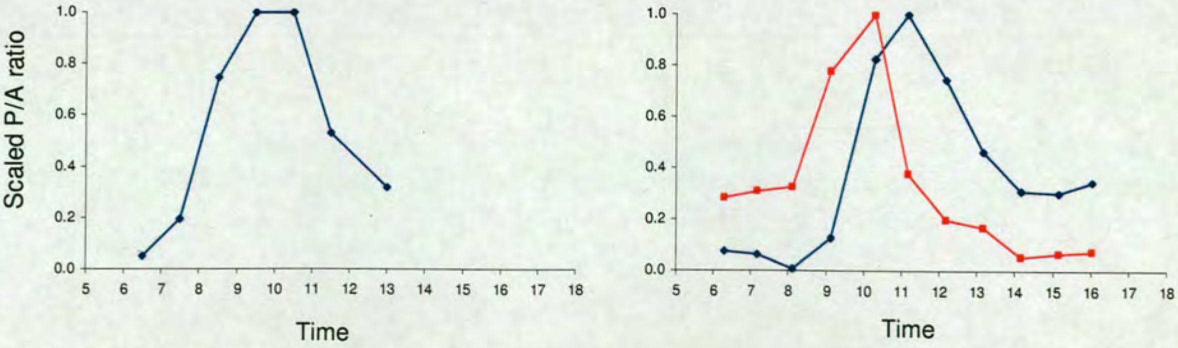
(k) Turkana Boma, 13th Sep 2004

2.18; 1.55

(l) Turkana Boma, 13th March 2004

1.62

Figure 4.4 (cont.) Daily patterns of pollen availability for individual trees of *V. etbaica* sampled on each day (a-l). The maximum absolute pollen to anther ratio for each tree is shown above the graph.



(a) Mongoose, 6th June 1999

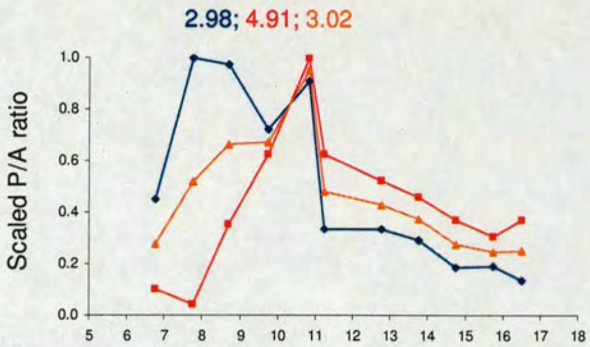
1.64

(b) Mongoose, 12th June 1999

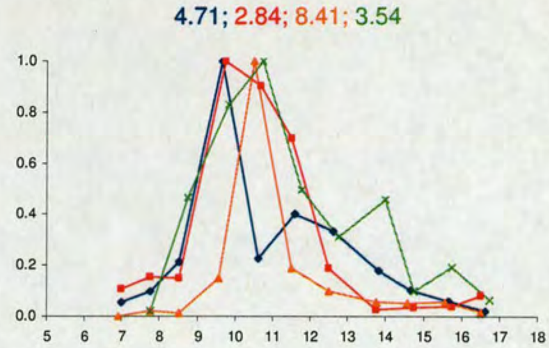
2.25; 3.01

Figure 4.5 Daily patterns of pollen availability for individual trees of *V. gerrardii* sampled on each day (a-i). The maximum absolute pollen to anther ratio for each tree is shown above the graph.

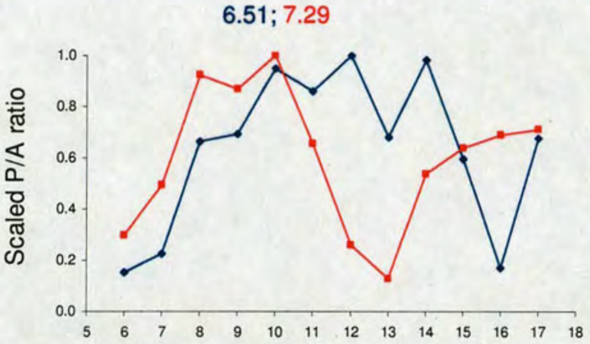
(c) High Dam, 16th June 1999



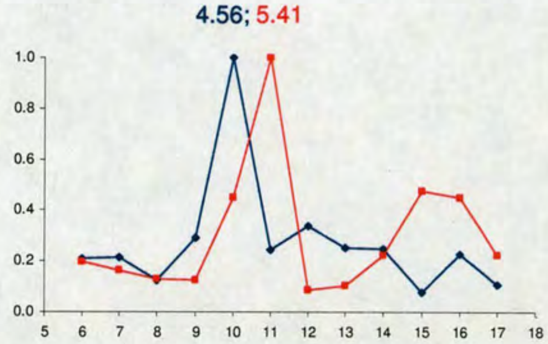
(d) High Dam, 17th June 1999



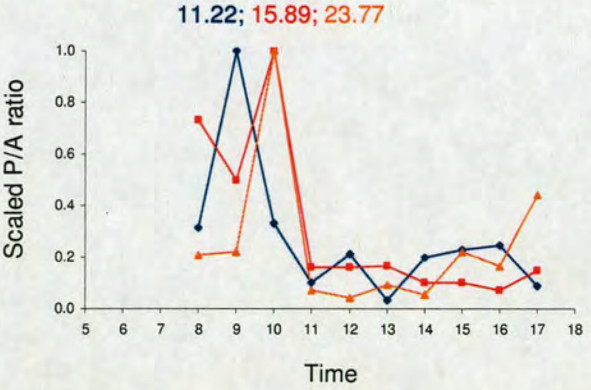
(e) Turkana Boma, 21st June 1999



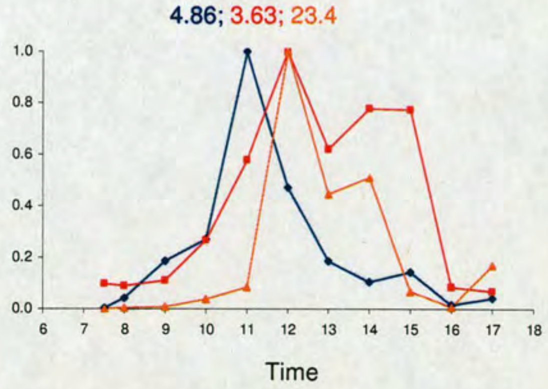
(f) Junction, 5th June 2003



(g) Junction, 18th March 2004



(h) High Dam, 28th July 2004



(i) Junction, 30th July 2004

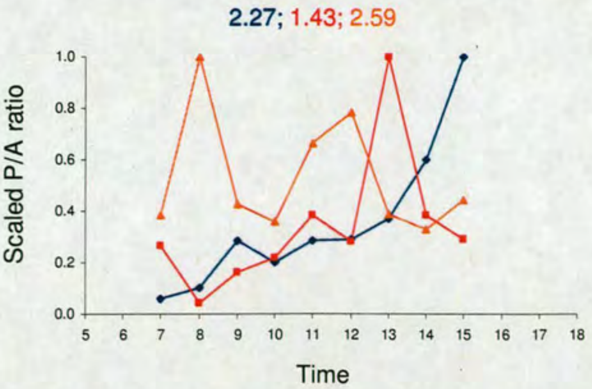
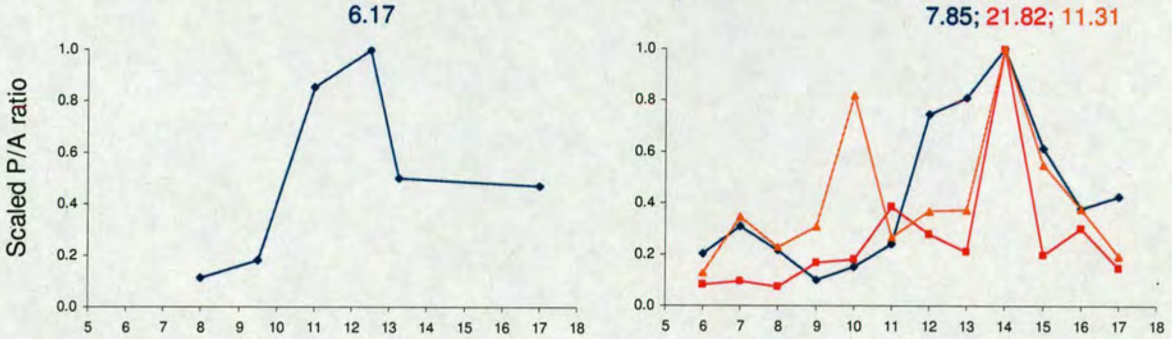
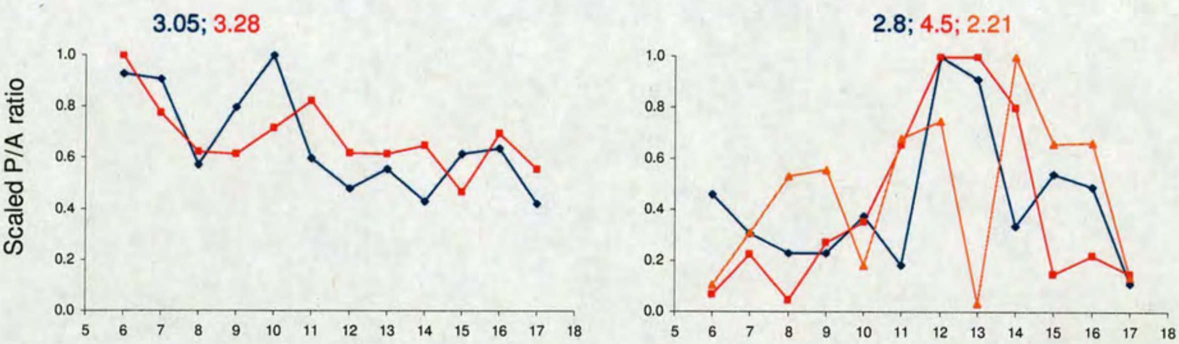


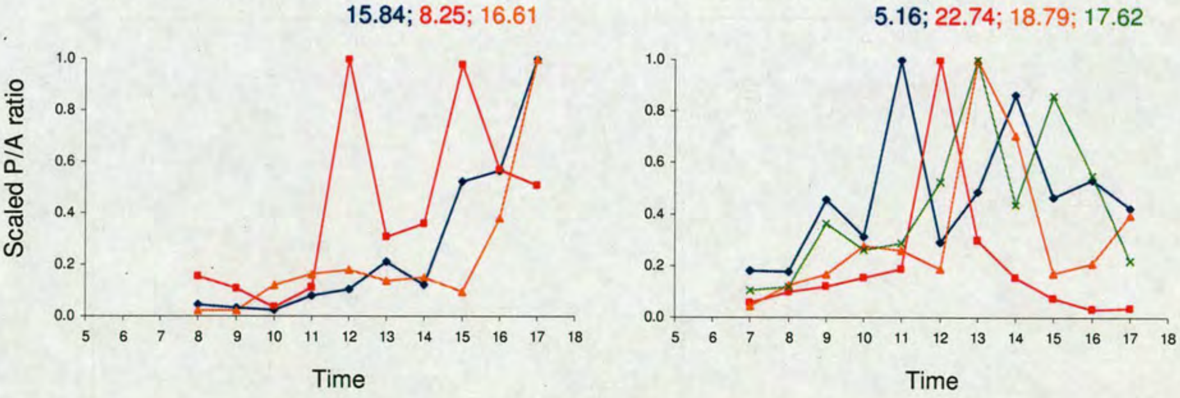
Figure 4.5 (cont.) Daily patterns of pollen availability for individual trees of *V. gerrardii* sampled on each day (a-i). The maximum absolute pollen to anther ratio for each tree is shown above the graph.


(a) Turkana Boma, 4th May 1998

(b) Mukenya, 29th September 2002


(c) Turkana Boma, 7th Nov 2003

(d) MRC, 27th March 2004


(e) MRC, 16th Feb 2005

(f) Turkana Boma, 16th March

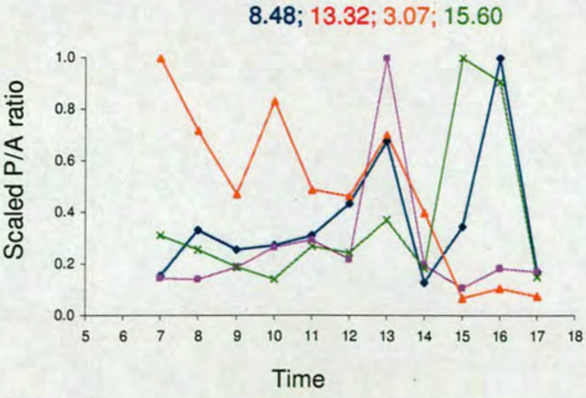
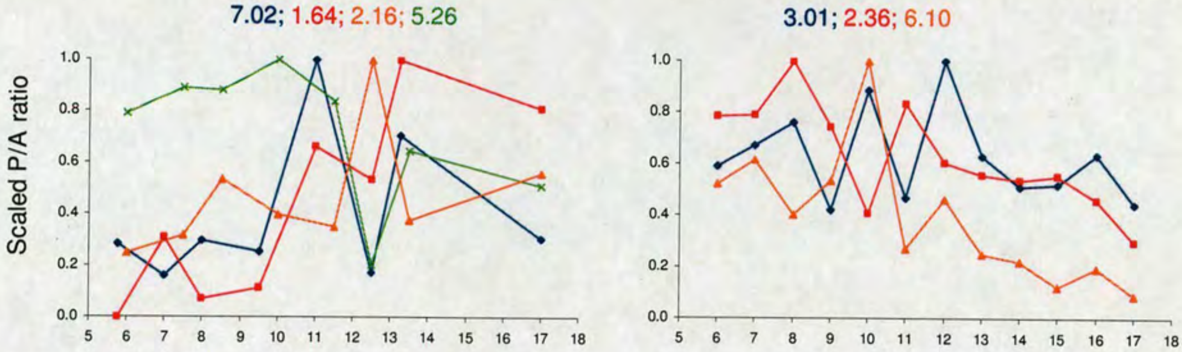

(g) Turkana Boma, 18th March

Figure 4.6 Daily patterns of pollen availability for individual trees of *S. mellifera* sampled on each day (a-g). The maximum absolute pollen to anther ratio for each tree is shown above the graph.

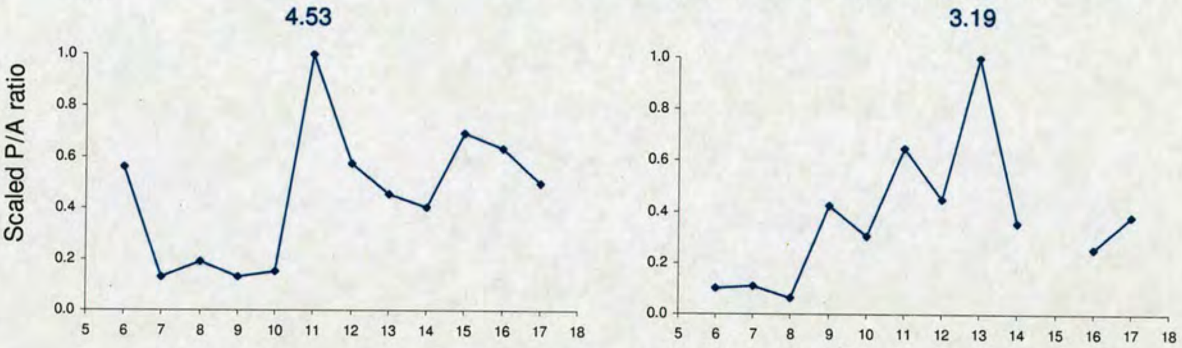
(a) Turkana Boma, 4th May 1998

(b) Mukenya, 9th Jan 2003



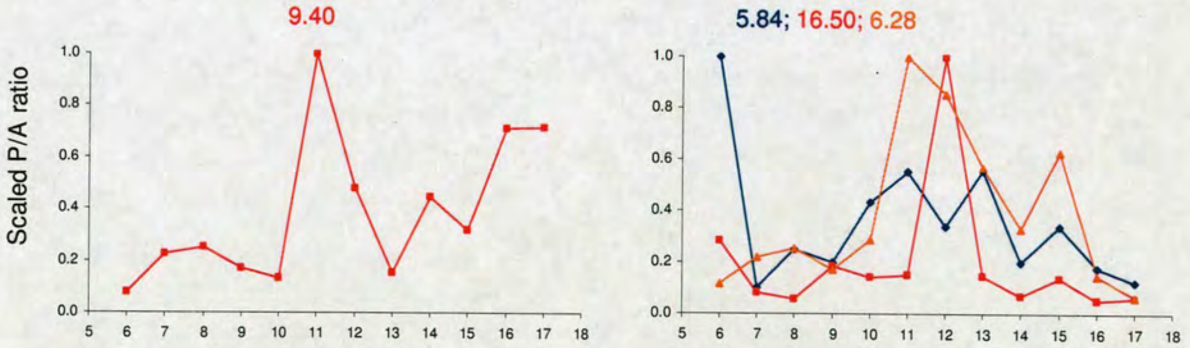
(c) MRC, 14th June 2003

(d) Turkana Boma, 14th June 2003



(e) Turkana Boma, 16th June 2003

(f) Turkana Boma, 19th June 2003



(g) Turkana Boma, 21st June 2004

(h) Turkana Boma, 22nd June 2004

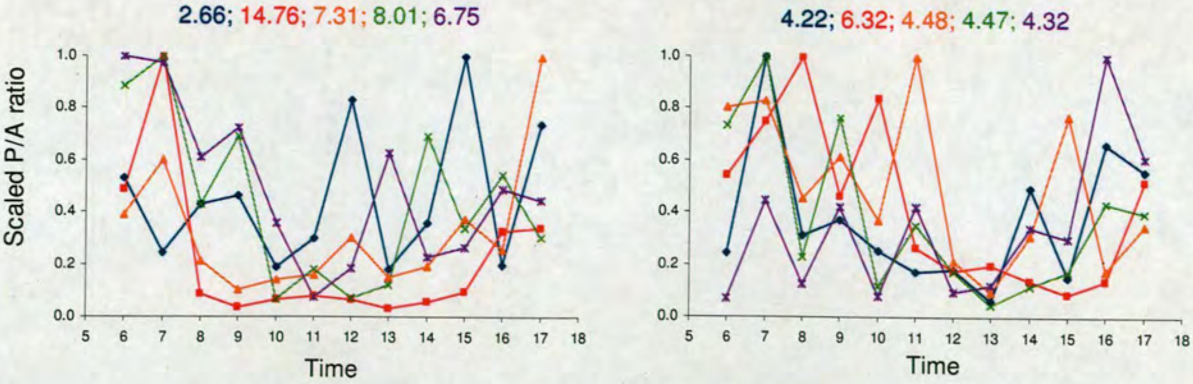
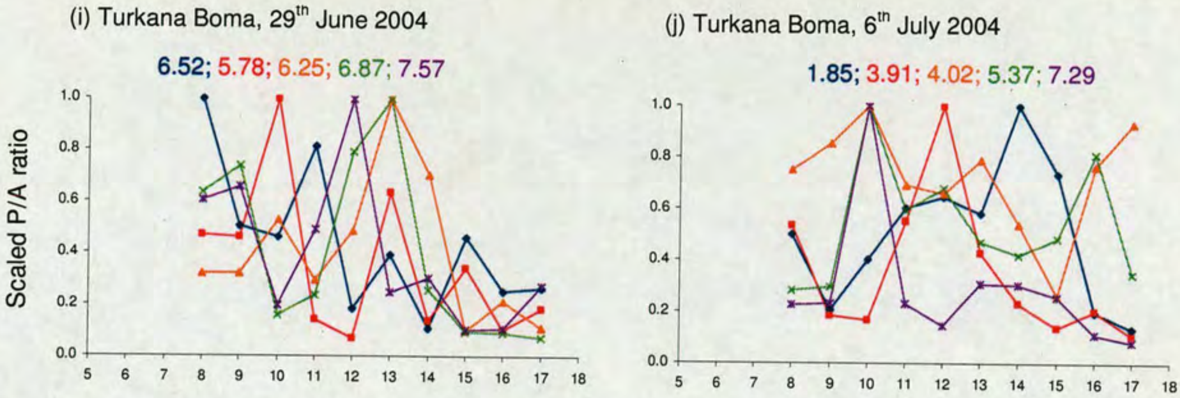
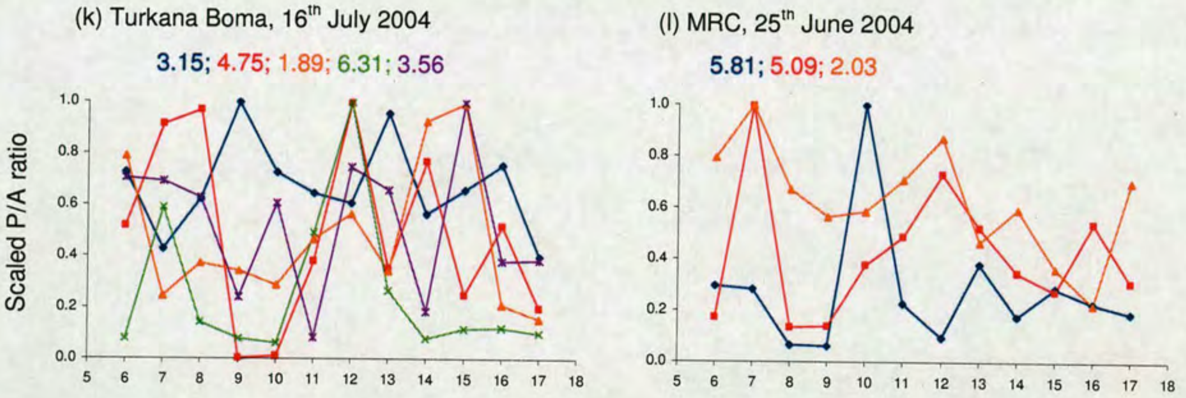


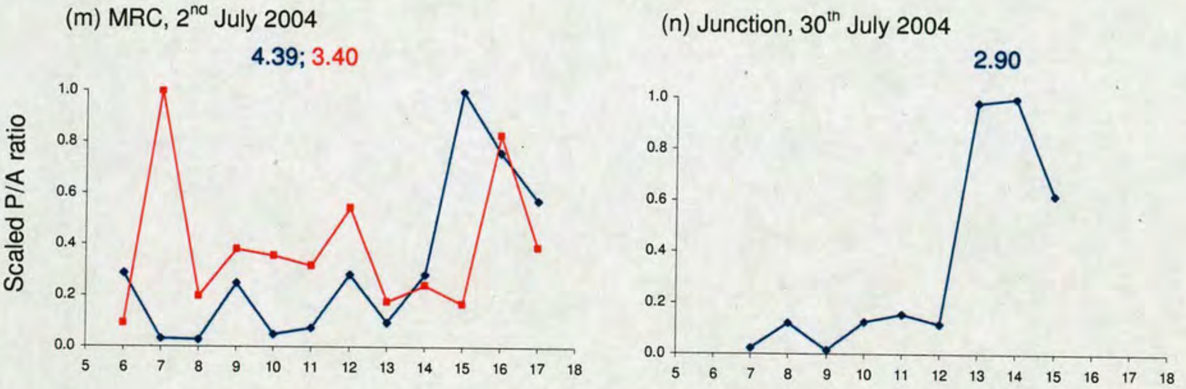
Figure 4.7 Daily patterns of pollen availability for individual trees of *V. nilotica* sampled on each day (a-o). The maximum absolute pollen to anther ratio for each tree is shown above the graph.


(i) Turkana Boma, 29th June 2004

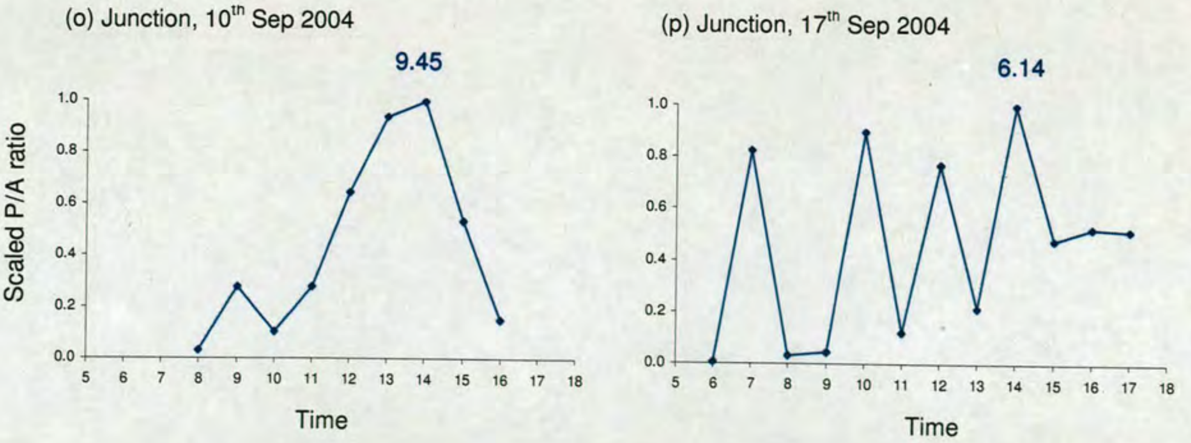
(j) Turkana Boma, 6th July 2004


(k) Turkana Boma, 16th July 2004

(l) MRC, 25th June 2004

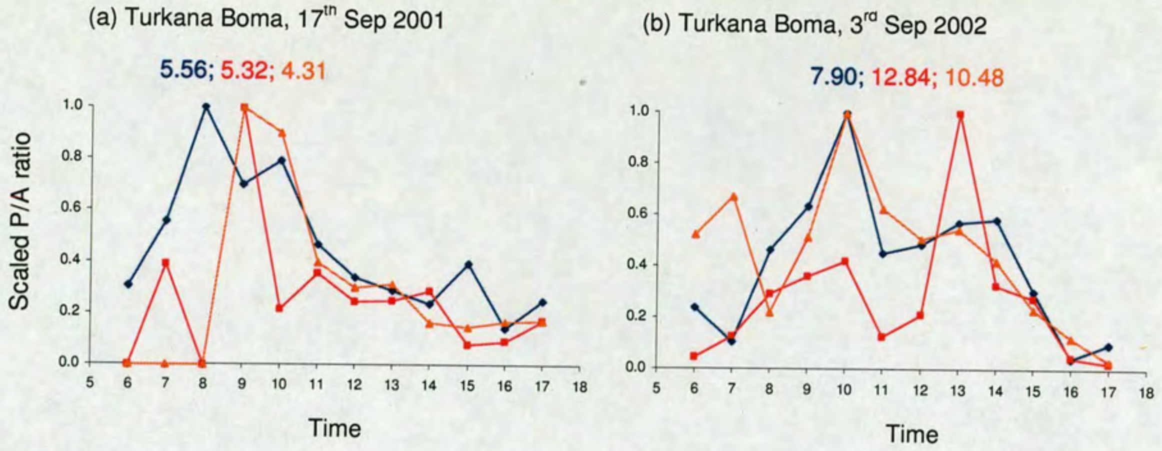

(m) MRC, 2nd July 2004

(n) Junction, 30th July 2004


(o) Junction, 10th Sep 2004

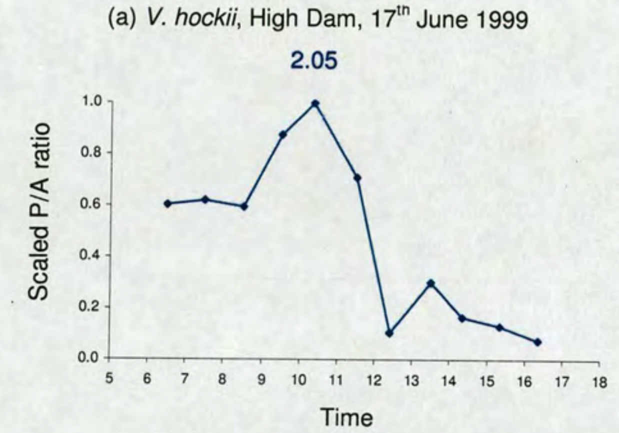
(p) Junction, 17th Sep 2004

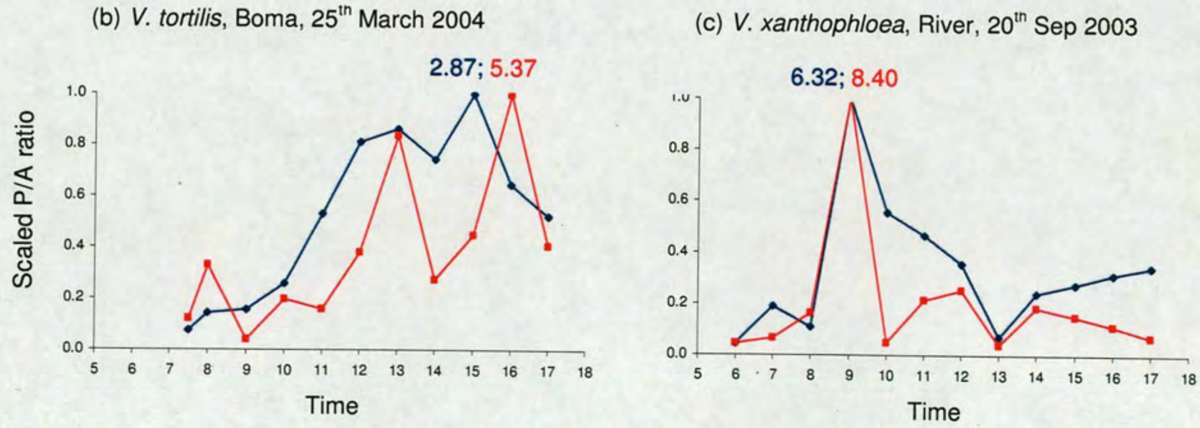
Figure 4.7 (cont.) Daily patterns of pollen availability for individual trees of *V. nilotica* sampled on each day (a-o). The maximum absolute pollen to anther ratio for each tree is shown above the graph.


(a) Turkana Boma, 17th Sep 2001

(b) Turkana Boma, 3rd Sep 2002

Figure 4.8 Daily patterns of pollen availability for individual trees of *V. seyal* sampled on each day (a-b). The maximum absolute pollen to anther ratio for each tree is shown above the graph.


(a) *V. hockii*, High Dam, 17th June 1999


(b) *V. tortilis*, Boma, 25th March 2004

(c) *V. xanthophloea*, River, 20th Sep 2003

Figure 4.9 Daily patterns of pollen availability for individual trees of (a) *V. hockii*, (b) *V. tortilis* and (c) *V. xanthophloea*. The maximum absolute pollen to anther ratio for each tree is shown above the graph.

*(b) Do individual trees show synchrony in the timing of dehiscence across days and seasons?*

Individual trees of *S. brevispica*, *V. drepanolobium*, *V. etbaica*, *V. gerrardii*, *S. mellifera* and *V. nilotica* were sampled on multiple days within a single flowering season or in different years (Table 4.4, Fig. 4.10).

Table 4.4. Dates of sampling for individual trees sampled on more than one day.

| Species | Site | Number of trees | Dates |
|---|---|---|---|
| *S. brevispica* | Mpala | 2 | 28th May 2005, 31st May 2005 |
| | Turkana Boma | 1 | 13th May 2003, 23rd Sep 2003 |
| | High Dam | 1 | 9th June 1999, 16th June 1999 |
| *V. drepanolobium* | Turkana Boma | 1 | 6th Sep 2004, 13th Sep 2004 |
| | Junction | 1 | 30th July 2004, 10th Sep 2004<br>17th Sep 2004 |
| | | 1 | 10th Sep 2004, 17th Sep 2004 |
| *V. etbaica* | Mpala | 1 | 11th Aug 2003, 13th Aug 2003<br>2nd Aug 2004, 7th Aug 2004 |
| | | 1 | 13th Aug 2003<br>2nd Aug 2004, 7th Aug 2004 |
| | | 2 | 2nd Aug 2004, 7th Aug 2004 |
| *V. gerrardii* | Mongoose | 1 | 6th June 1999, 12th June 1999 |
| | Junction | 1 | 5th June 2003, 30th July 2004 |
| *S. mellifera* | Mpala | 3 | 27th March 2004, 16th Feb 2005 |
| *V. nilotica* | Mpala | 1 | 25th June 2004, 2nd July 2004 |
| | Junction | 1 | 30th July 2004, 10th Sep 2004<br>17th Sep 2004 |
| | Turkana Boma | 1 | 16th June 2003, 19th June 2003<br>21st June 2004, 22nd June 2004<br>29th June 2004, 6th July 2004<br>16th July 2004 |
| | | 1 | 19th June 2003, 21st June 2004<br>6th July 2004, 16th July 2004 |
| | | 1 | 21st June 2004, 22nd June 2004<br>29th June 2004, 6th July 2004<br>16th July 2004 |
| | | 1 | 22nd June 2004, 29th June 2004 |
| | | 2 | 22nd June 2004, 29th June 2004<br>6th July 2004 |

*(i) Variation across days within the same flowering season*

Several trees showed remarkable consistency in the timing of dehiscence and maximum pollen availability between days in the same flowering season (Fig. 4.10a, d, e, g). However, most trees showed different dehiscence patterns on different days. Some trees peaked at the same time on different days but differed in their patterns of dehiscence. For example, a *V. nilotica* tree sampled at Junction in 2004 had its pollen availability peak at approximately 14.00 on three days, despite a variable pattern of dehiscence on September 17th (Fig. 4.10p).

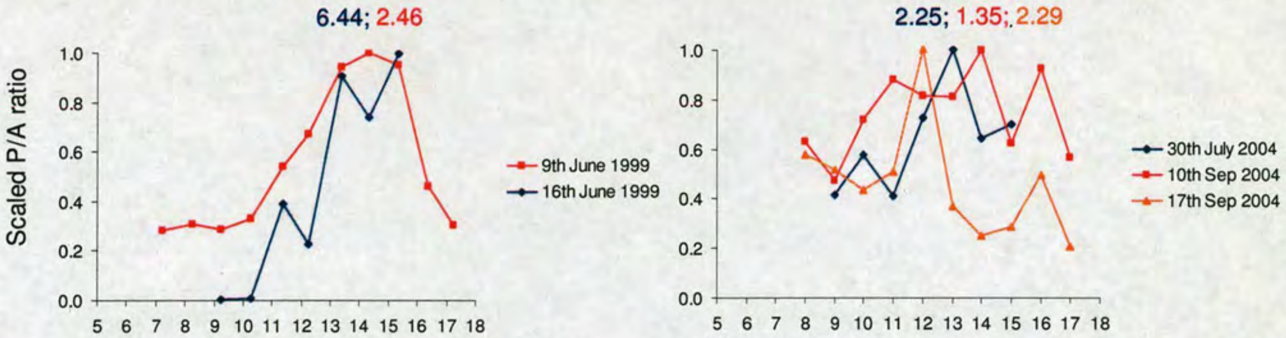
Perhaps the most complex patterns were produced by a group of *V. nilotica* trees sampled at Turkana Boma in 2004. The pollen availability patterns were highly variable and there was little consistency between trees sampled on individual days (Fig. 4.7g-k) or individual trees between days (Fig. 4.10r-x). Relatively high pollen to anther ratios often occurred early in the morning (6.00-8.00) and at the end of a sampling day (17.00). All trees showed a pollen availability peak between 11.00 and 13.00 on the majority of days on which they were sampled, although for most trees this was not the highest peak. Some trees displayed trends across sampling days. Pollen availability peaks with similar pollen to anther ratios were observed at 13.00 for tree N5 on three of the four sampling days and between 9.00 and 10.00 on all four days (Fig. 4.10u). Tree N3 had peaks between 11.00 and 12.00 on three sampling days in 2004, although the peak on 21st June was relatively small in comparison to other peaks on that day (Fig. 4.10r).

*(ii) Variation across days between years*

*Vachellia etbaica*, *V. gerrardii*, *S. mellifera* and *V. nilotica* individuals were sampled across years. Although some trees showed similar patterns of pollen availability across years, the majority of trees varied in their timing of maximum pollen availability (Fig. 4.10 h-j, m-o, r).

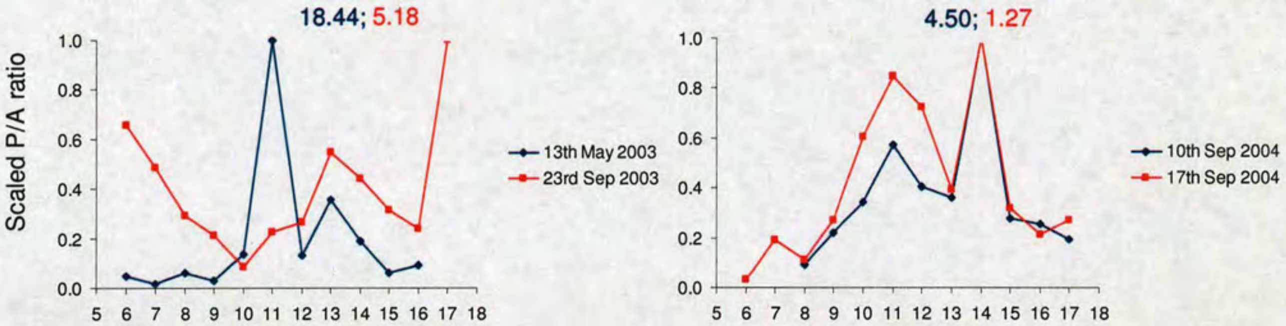
(a) *A. brevispica*, High Dam

(b) *V. drepanolobium* (tree 1), Junction



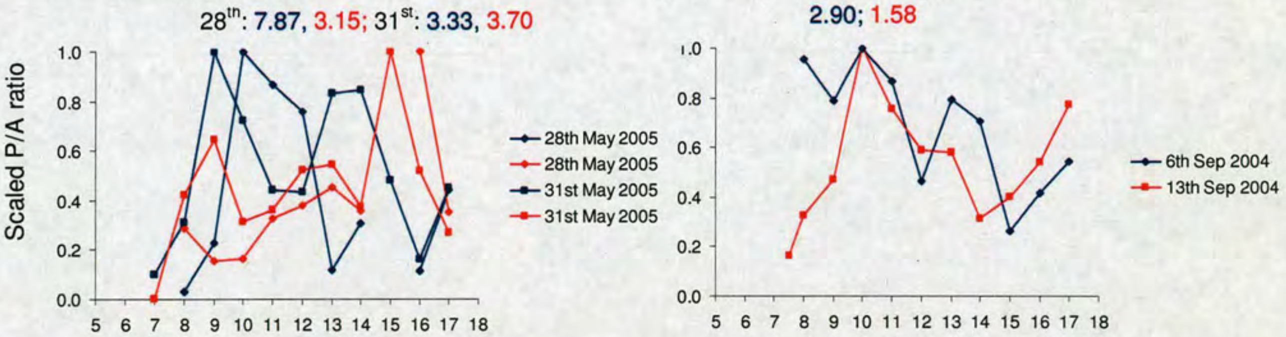
(c) *A. brevispica*, Turkana Boma

(d) *V. drepanolobium* (tree 3), Junction



(e) *A. brevispica*, MRC

(f) *V. drepanolobium*, Turkana Boma



(g) *V. gerrardii*, Mongoose

(h) *V. gerrardii*, Junction

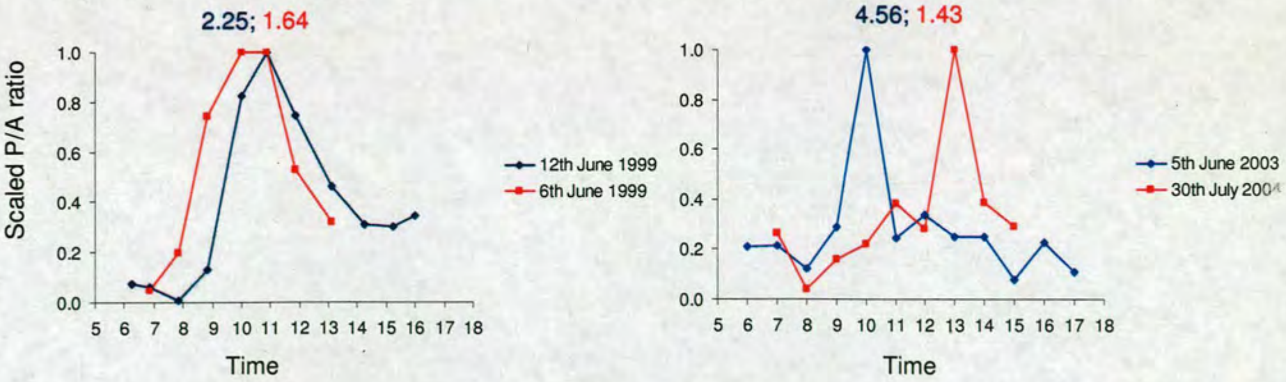
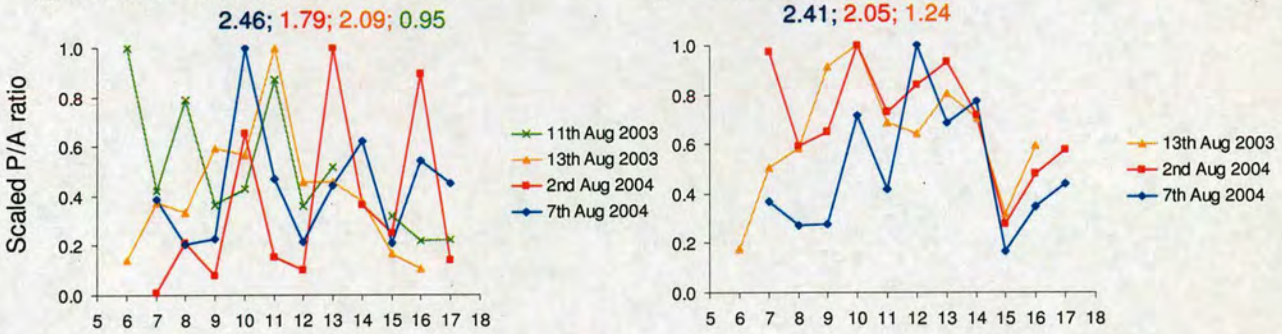
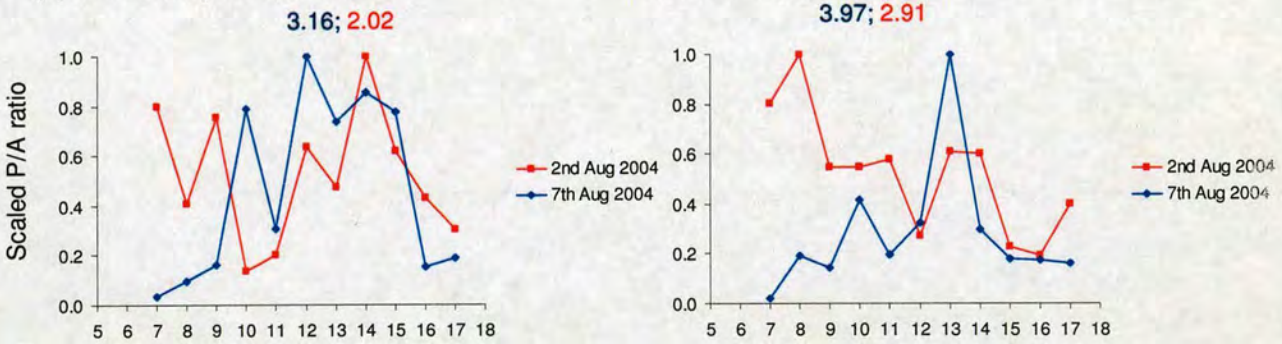


Figure 4.10 Daily patterns of pollen availability for individual acacia trees sampled on multiple days (a-x). The maximum absolute pollen to anther ratio for each tree is shown above the graph.



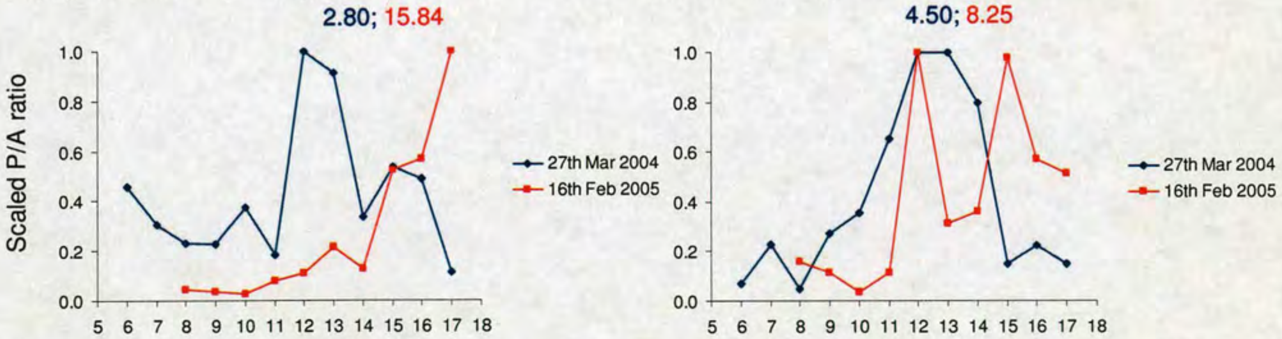
(i) *V. etbaica* (tree 1), MRC

(j) *V. etbaica* (tree 2), MRC



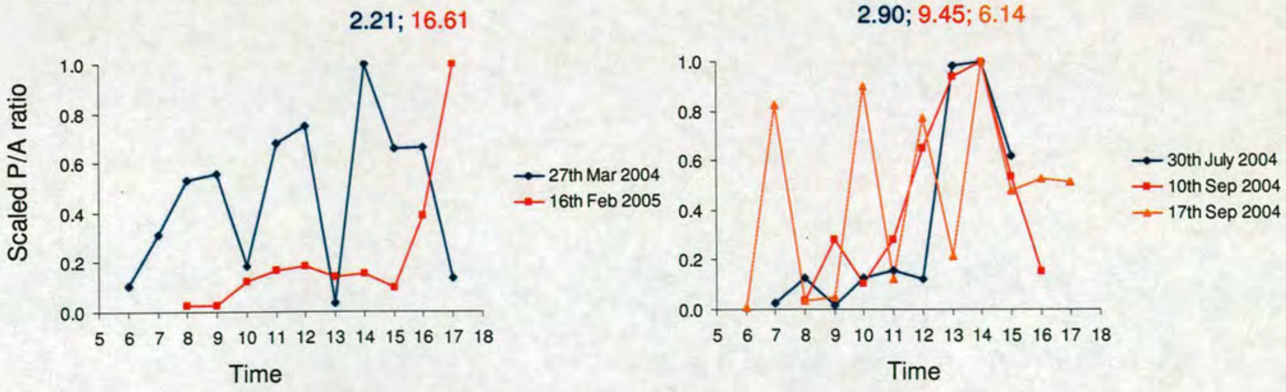
(k) *V. etbaica* (tree 3), MRC

(l) *V. etbaica* (tree 4), MRC



(m) *S. mellifera* (tree 1), MRC

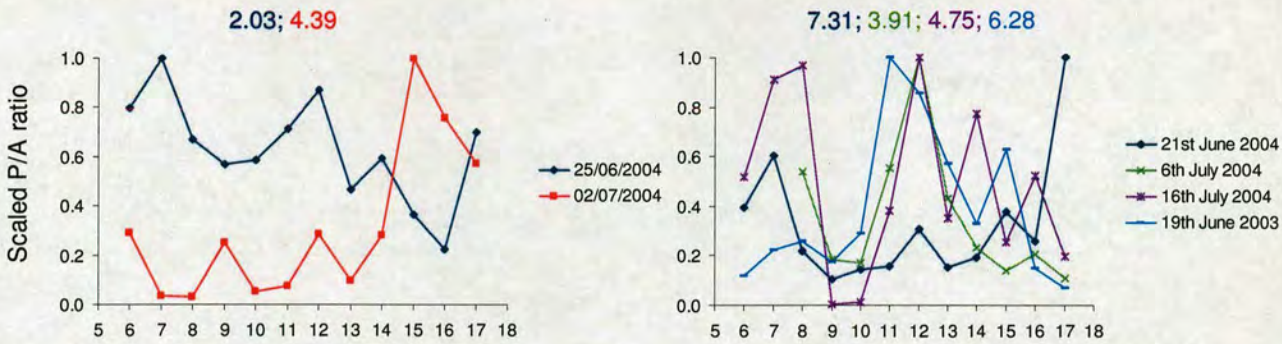
(n) *S. mellifera* (tree 2), MRC



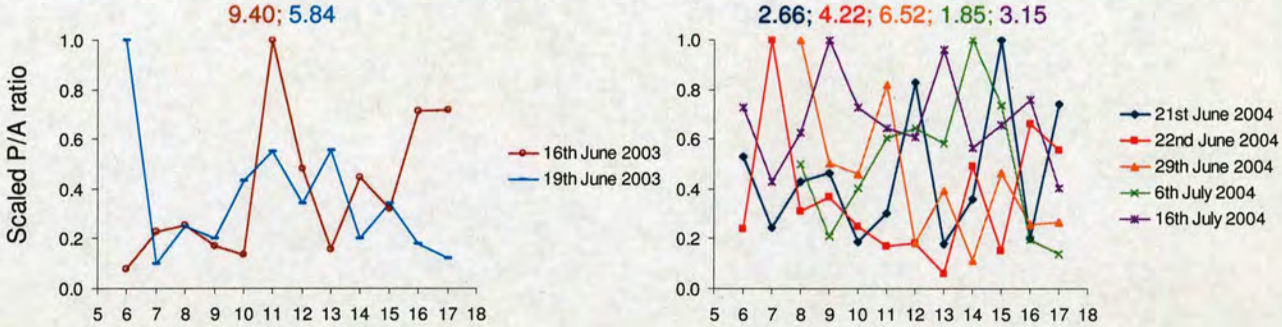
(o) *S. mellifera* (tree 3), MRC

(p) *V. nilotica*, Junction

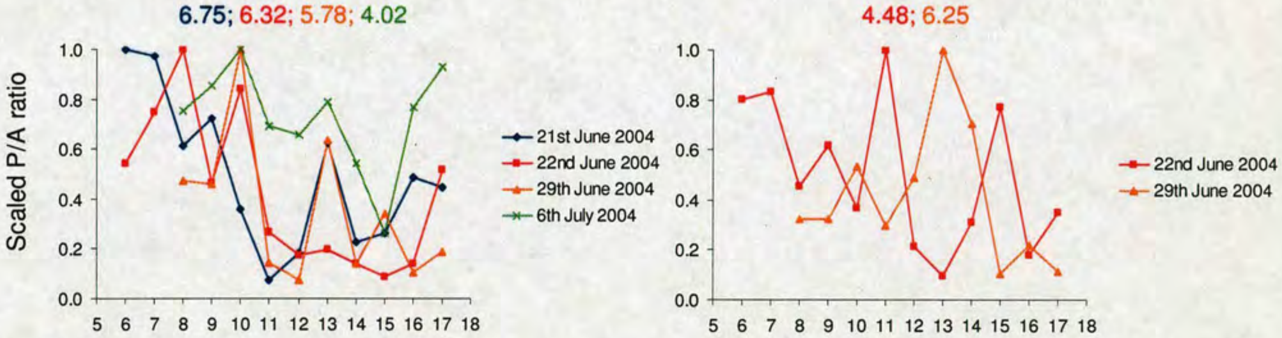
Figure 4.10 (cont.) Daily patterns of pollen availability for individual acacia trees sampled on multiple days (a-x). The maximum absolute pollen to anther ratio for each tree is shown above the graph.


(q) *V. nilotica*, MRC

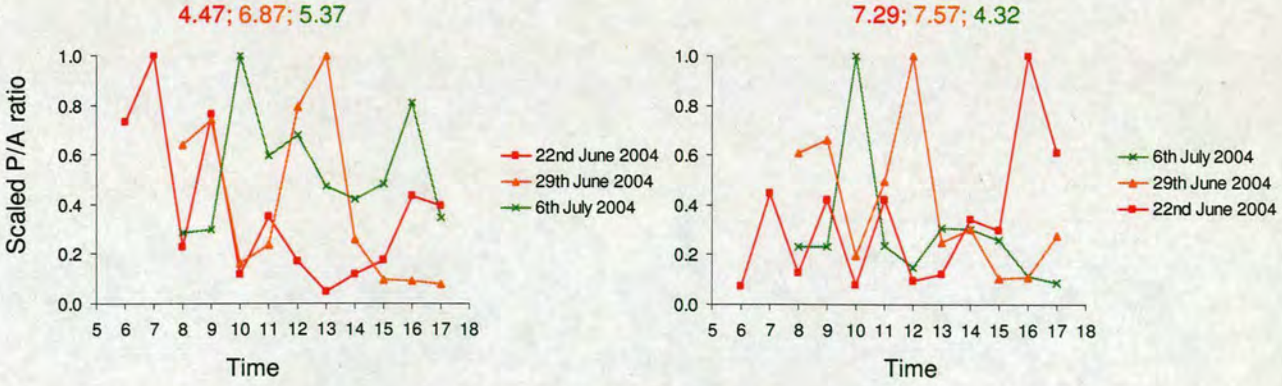
(r) *V. nilotica* (tree 3), Turkana Boma


(s) *V. nilotica* (tree 1), Turkana Boma

(t) *V. nilotica* (tree 1 cont.), Turkana Boma


(u) *V. nilotica* (tree 5), Turkana Boma

(v) *V. nilotica* (tree 6), Turkana Boma


(w) *V. nilotica* (tree 7), Turkana Boma

(x) *V. nilotica* (tree 8), Turkana Boma

Figure 4.10 (cont.) Daily patterns of pollen availability for individual acacia trees sampled on multiple days (a-x). The maximum absolute pollen to anther ratio for each tree is shown above the graph.

*(c) Is there synchrony in the timing of dehiscence for each species within and between sites?*

Most acacia species showed a large amount of variation in the timing of maximum pollen availability among sampling days at each site (Figs. 4.11-4.17). *Vachellia gerrardii* showed the most consistent patterns of pollen availability among sampling days at each site and across all sampling sites (Fig 4.15). Excluding the trees sampled on 30th July 2004 at Junction site, the mean pollen availability peak across all trees on sampling days at Mongoose, Junction and Turkana Boma sites occurred at 10.00 and varied between 11.00 and 12.00 at High Dam (Fig. 4.15, Table 4.5). *Vachellia seyal* had similar mean patterns of pollen availability across trees on two sampling days at Turkana Boma with a mean pollen availability peak across trees at 9.00 on 17th September 2001 and 10.00 on 3rd September 2002 (Fig. 4.13).

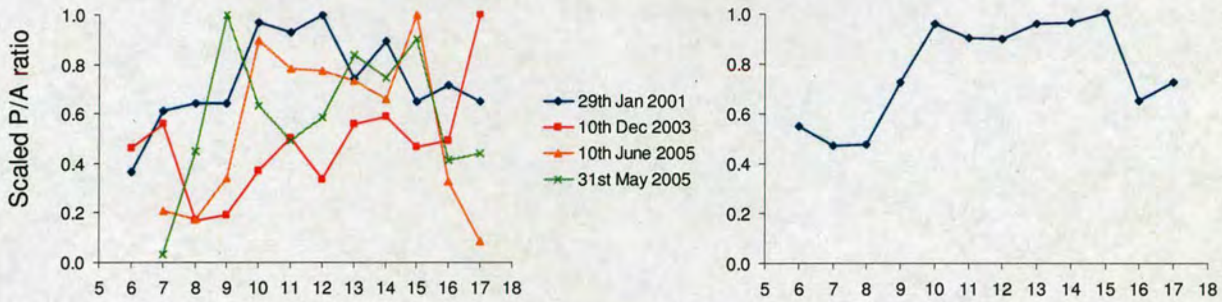
*S. brevispica*, *V. drepanolobium*, *V. etbaica*, *S. mellifera* and *V. nilotica* showed more variation among days, although for all except *V. nilotica*, site means calculated across all sampling days showed some similarities between sites (Figs. 4.11, 4.12, 4.14, 4.16). Although *S. brevispica* varied among days, the mean patterns of pollen availability across days at each site peaked between 14.00 and 16.00 at all sites (Fig. 4.11, Table 4.5). *V. drepanolobium* also had similar patterns of dehiscence across sites, with the mean pollen availability across all days peaking at 10.00 at both Turkana Boma and Junction, although slightly larger peaks occurred at 12.00 and 14.00 at Junction (Fig. 4.12, Table 4.5). Mean patterns of pollen availability for *V. etbaica* at MRC, Turkana Boma and Mukenya all showed peaks at 10.00, although larger peaks occurred later at MRC and Mukenya (Fig. 4.14, Table 4.5). Mean pollen availability peaks for *S. mellifera* occurred between 12.00 and 14.00 across sites (Fig. 4.15, Table 4.5).

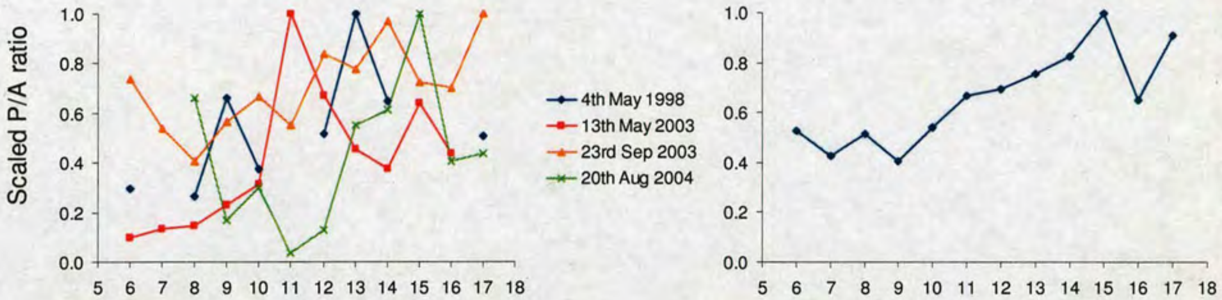
*Vachellia nilotica* was the most variable species across sampling days and across sites (Fig. 4.17). At MRC, variation among individual trees on each day resulted in pollen availability patterns with three peaks (early morning, middle of the day, and late afternoon) for both the mean patterns for each day and for the whole site (Fig. 4.17a, e). At Turkana Boma, the pollen availability peak for the overall site mean occurred at 11.00 (Fig. 4.17f). However high pollen availabilities for individual trees at the start or end of sampling days (see Fig. 4.7) meant that the mean patterns for some sampling days and the overall site mean had smaller peaks at these times (Figs. 4.17b, c, f). *Vachellia nilotica* showed the most consistent pattern of pollen availability at Junction, with a single individual tree peaking at 14.00 on all three sampling days, however no other trees of this species were sampled at this site (Figs. 4.17d, h).

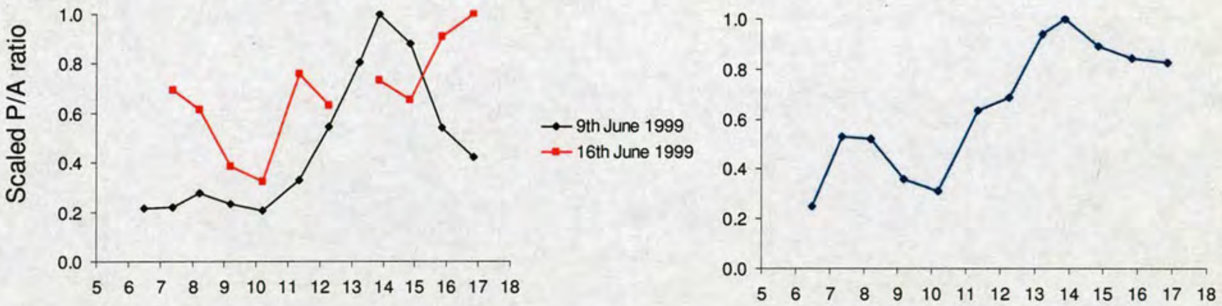
Table 4.5 Time of maximum pollen availability for acacia species at each site. On each sampling day the mean pollen availability at each time was calculated across all sampled trees and for each site the mean pollen availability was calculated across all sampling days. ns indicates that a species was present at that site, but was not sampled. The overall mean was calculated across all sampling sites at Mpala.

| | MRC | Turkana | Mongoose | Mukenya | Junction | High Dam | Boma | Overall |
|---|---|---|---|---|---|---|---|---|
| *S. brevispica* | 15.00 | 15.00 | ns | ns | 15.00 | 14.00 | 16.00 | 15.00 |
| *V. drepanolobium* | - | 10.00 | ns | - | 12.00 | - | - | 10.00 |
| *V. etbaica* | 13.00 | 10.00 | - | 12.00 | ns | - | ns | 10.00 |
| *V. gerrardii* | - | 10.00 | 10.00 | - | 10.00 | 10.45 | - | 10.00 |
| *V. hockii* | - | - | - | - | ns | 10.00 | - | 10.00 |
| *S. mellifera* | 12.00 | 13.00 | ns | 14.00 | ns | ns | ns | 14.00 |
| *V. nilotica* | 16.00 | 11.00 | - | 10.00 | 14.00 | ns | ns | 12.00 |
| *V. seyal* | - | 10.00 | - | - | ns | - | - | 10.00 |
| *V. tortilis* | - | - | - | - | - | - | 13.00 | 13.00 |
| *V. xanthophloea* | - | - | - | - | - | - | - | 9.00* |

* *V. xanthophloea* was sampled at River site.


(a) MRC, means across trees per day
(e) MRC, means across sampling days


(b) Turkana Boma, means across trees per day
(f) Turkana Boma, means across sampling days


(c) High Dam, means across trees per day
(g) High Dam, means across sampling days

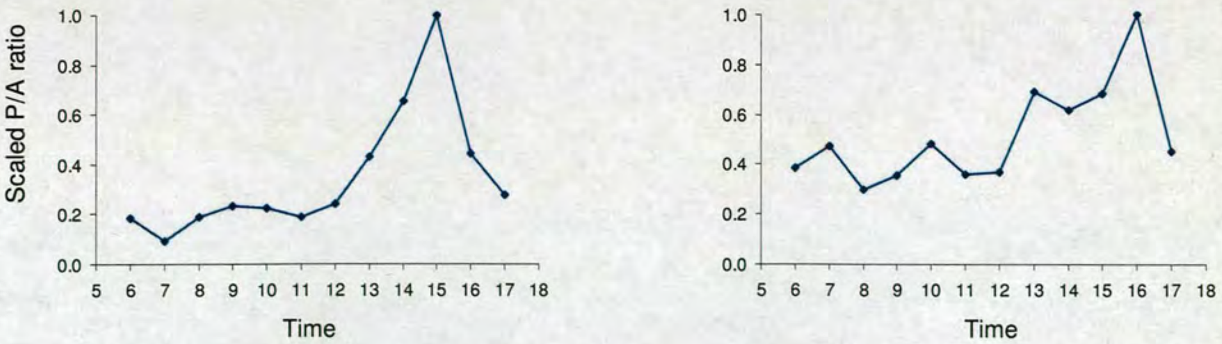
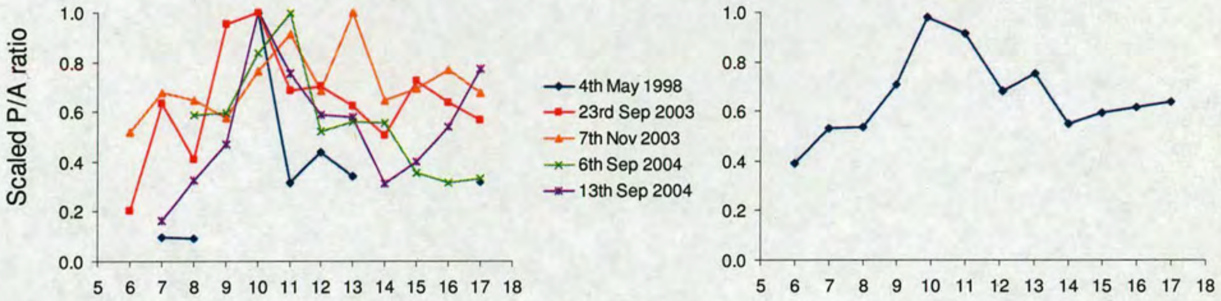

(d) Junction, means across trees on 5<sup>th</sup> June 2003
(h) Boma, means across trees on 27<sup>th</sup> Sep 2003

Figure 4.11 Mean patterns of pollen availability for *S. brevispica* calculated across trees on each sampling day (a-c) and sampling days (d-h) at each site. At Junction and Boma sites *S. brevispica* was only sampled on one day, therefore only one graph is shown for these sites.

(a) Turkana Boma, means across trees per day

(c) Turkana Boma, means across sampling days



(b) Junction, means across trees per day

(d) Junction, means across sampling days

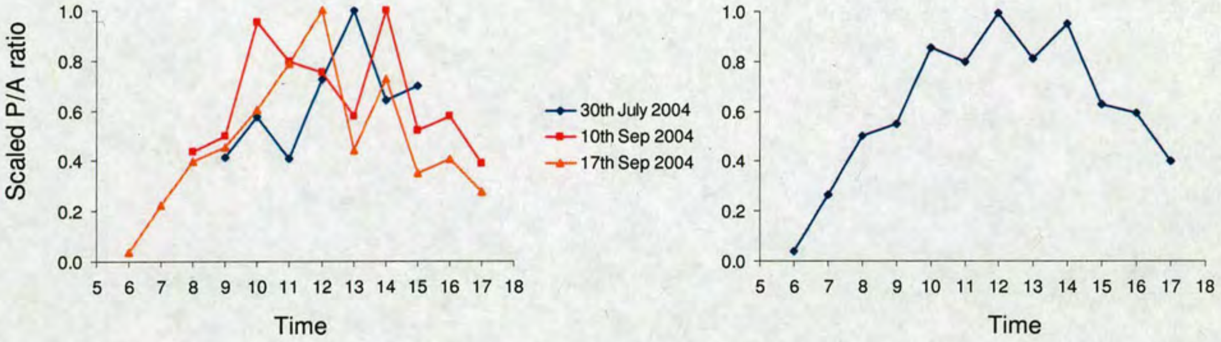


Figure 4.12 Mean patterns of pollen availability for *V. drepanolobium* calculated across trees on each sampling day (a-b) and sampling days (c-d) at each site.

(a) Turkana Boma, means across trees per day

(b) Turkana Boma, means across sampling days

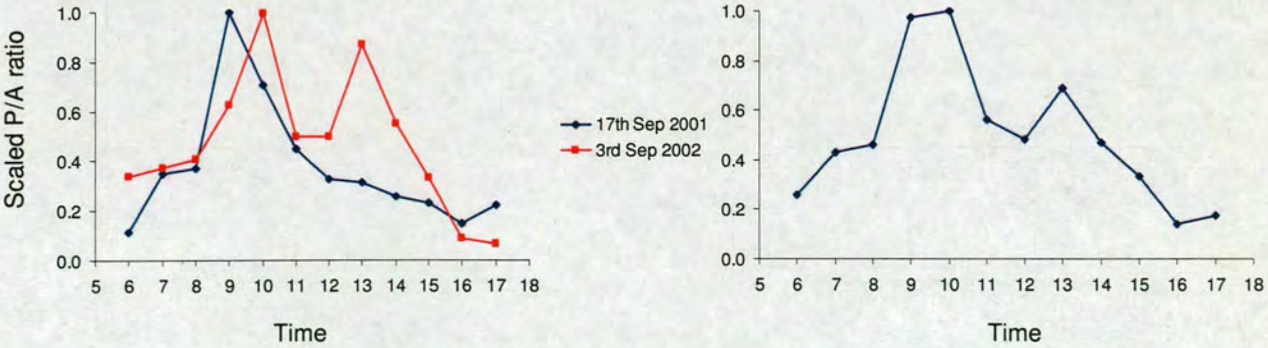
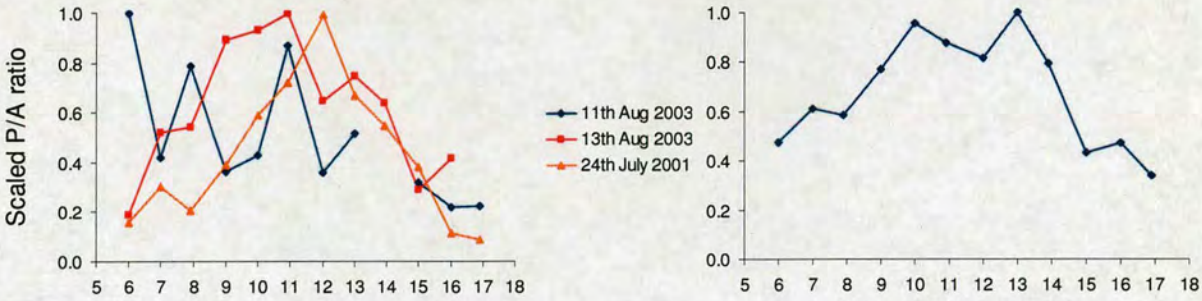


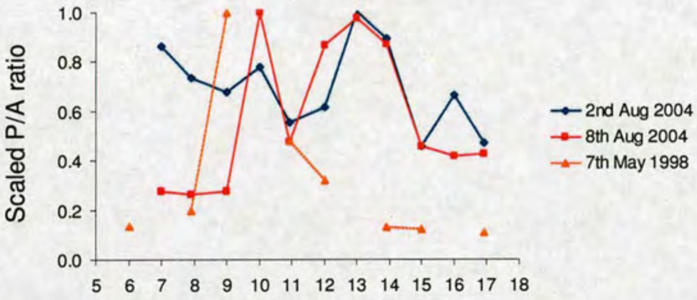
Figure 4.13 Mean patterns of pollen availability for *V. seyal* calculated across trees on each sampling day (a) and sampling days (b) at Turkana Boma.

(a) MRC, means across trees per day (1)

(e) MRC, means across sampling days

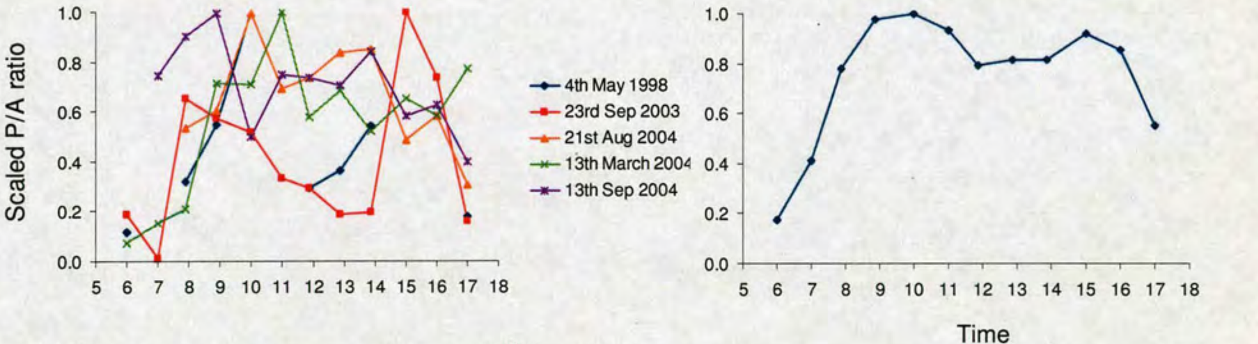


(b) MRC, means across trees per day (2)



(c) Turkana Boma, means across trees per day

(f) Turkana Boma, means across sampling days



(d) Mukenya, means across trees on 30$^{th}$ Aug 2002

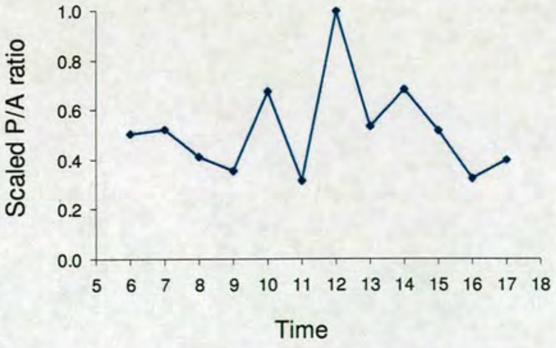
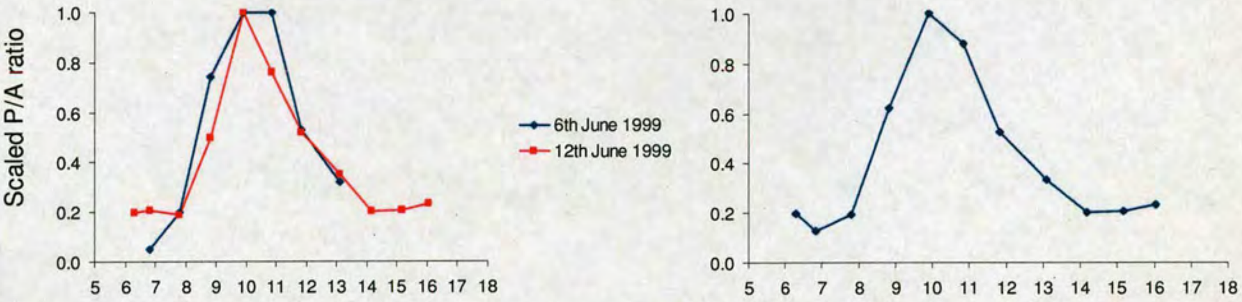


Figure 4.14 Mean patterns of pollen availability for *V. etbaica* calculated across trees on each sampling day (a-d) and sampling days (e-f) at each site. At Mukenya *V. etbaica* was only sampled on one day, therefore only one graph is shown for this site.

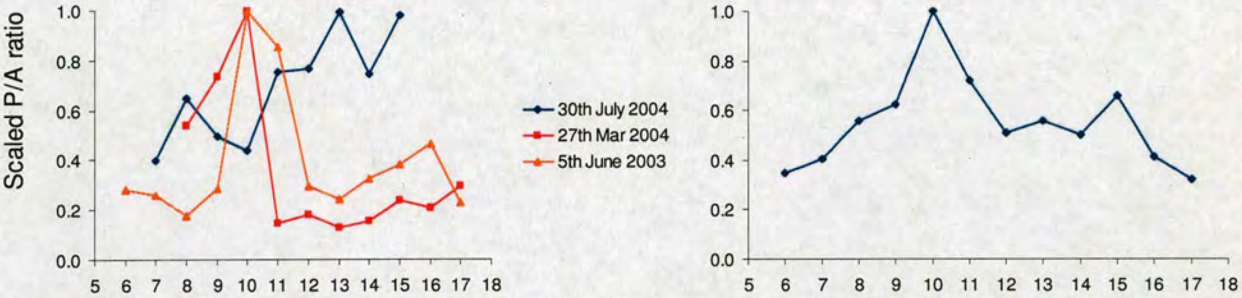
(a) Mongoose, means across trees per day

(e) Mongoose, means across sampling days



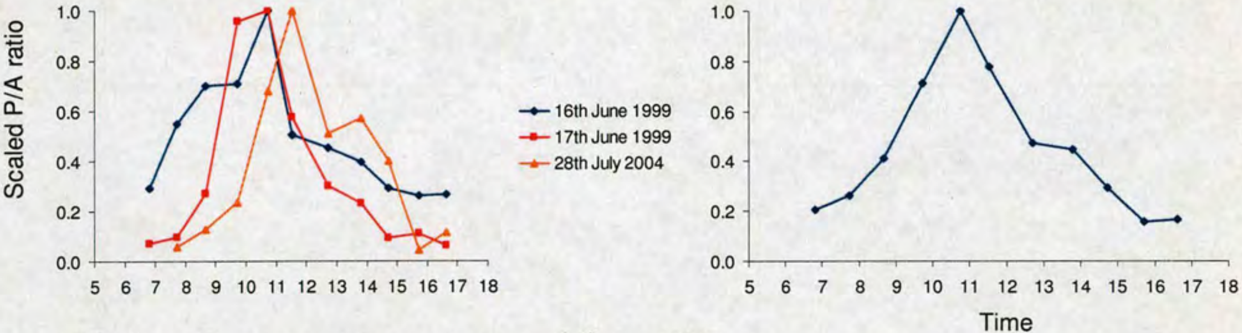
(b) Junction, means across trees per day

(f) Junction, means across sampling days



(c) High Dam, means across trees per day

(g) High Dam, means across sampling days



(d) Turkana Boma, mean across trees on 21st June 1999

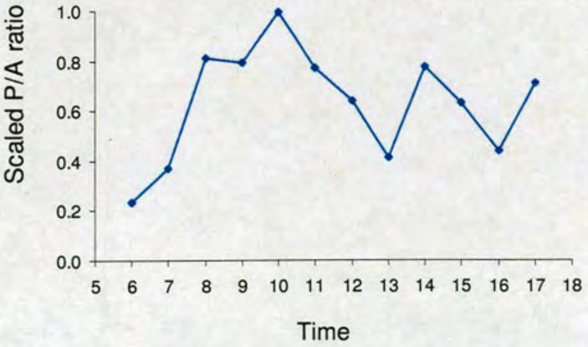
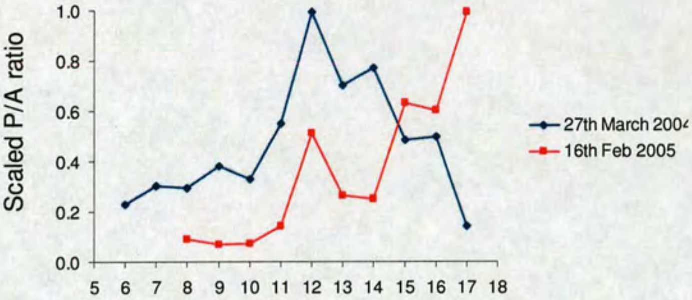
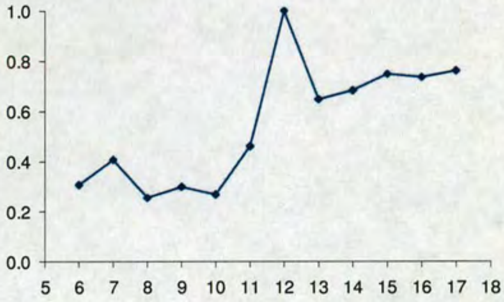


Figure 4.15 Mean patterns of pollen availability for *V. gerrardii* calculated across trees on each sampling day (a-d) and sampling days (e-g) at each site. At Turkana Boma *V. gerrardii* was only sampled on one day, therefore only one graph is shown for this site.

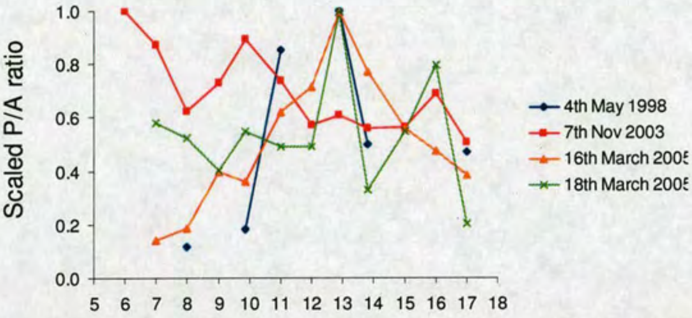
(a) MRC, means across trees per day



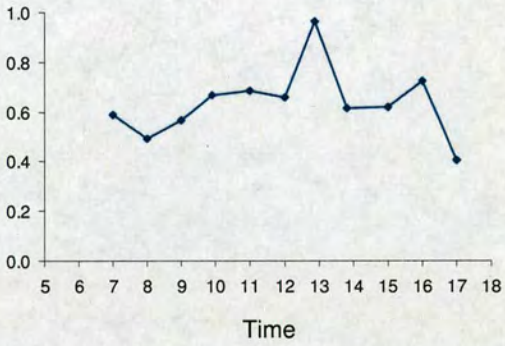
(d) MRC, means across sampling days



(b) Turkana Boma, means across trees per day



(e) Turkana Boma, means across sampling days



(c) Mukenya, means across trees on 29$^{th}$ Sep 2002

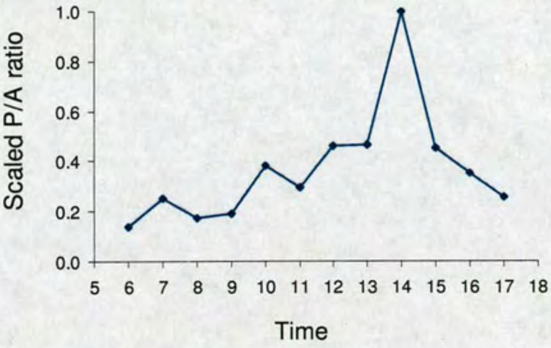
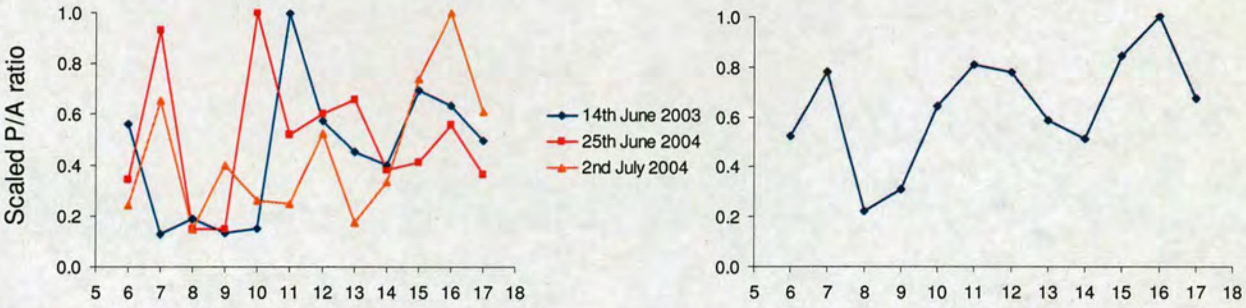
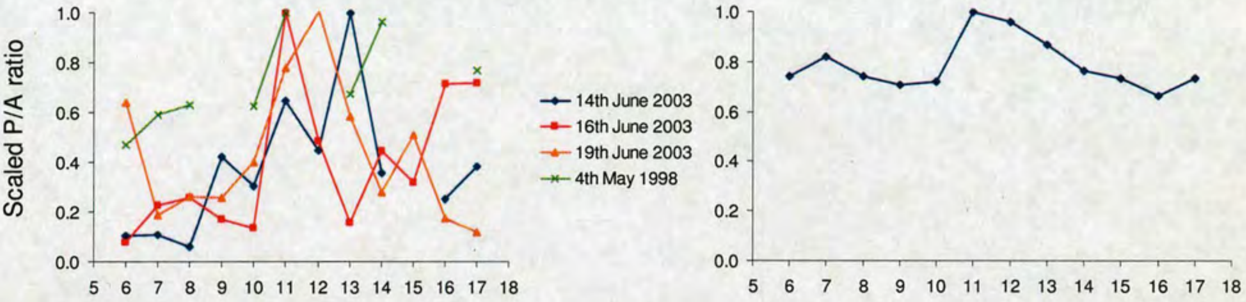


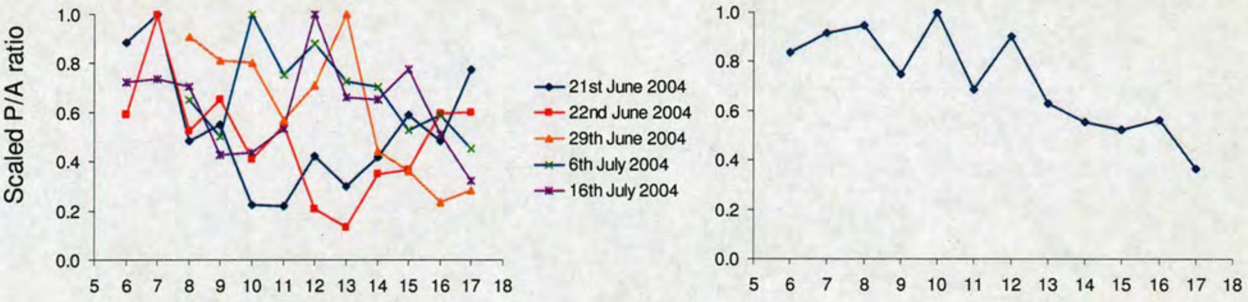
Figure 4.16 Mean patterns of pollen availability for *S. mellifera* calculated across trees on each sampling day (a-c) and sampling days (d-e) at each site. At Mukenya *S. mellifera* was only sampled on one day, therefore only one graph is shown for this site.


(a) MRC, means across trees per day

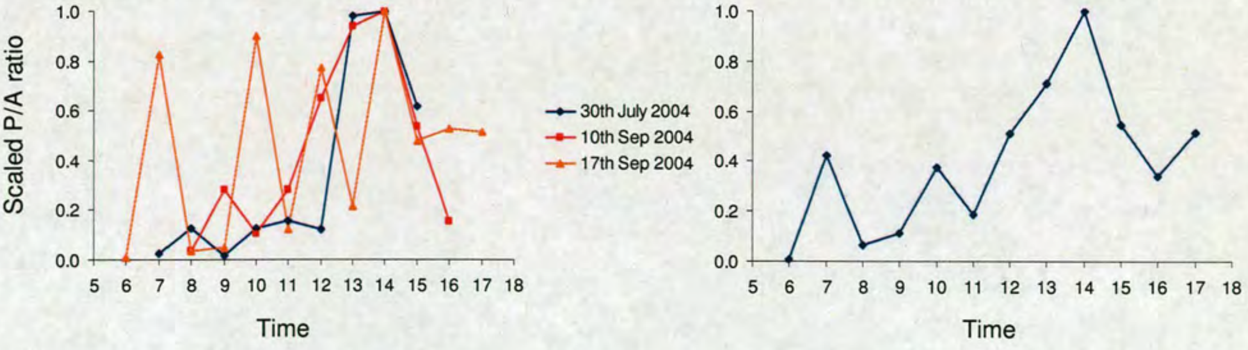
(e) MRC, means across sampling days


(b) Turkana Boma, means across trees per day (1)

(f) Turkana Boma, means across sampling days


(c) Turkana Boma, means across trees per days (2)

(g) Mukenya, means across trees on 9$^{th}$ Jan 2003


(d) Junction, means across trees per day

(h) Junction, means across sampling days

Figure 4.17 Mean patterns of pollen availability for *V. nilotica* calculated across trees on each sampling day (a-d) and sampling days (e-h) at each site. At Mukenya *V. nilotica* was only sampled on one day, therefore only one graph is shown for this site.

### 4.3.2 Can variation in the timing of dehiscence within species be explained by variation in relative humidity?

*(a) Daily patterns of microclimate variation*

Daily patterns of relative humidity and temperature were consistent between days and sites, although there was some variation in the range of values between days (Fig. 4.18). Relative humidity was generally lower during the dry season (Jan-March), although temperature varied less between seasons.

*(b) Does variation in relative humidity explain the variation in timing of dehiscence?*

Variation in the time of maximum pollen availability was not explained by variation in relative humidity for most species (Fig. 4.19). In *S. brevispica*, mean relative humidity during two two-hour time periods (11.00-13.00 and 12.00-14.00) had a significant negative effect on the timing of maximum pollen availability (Table 4.6). This meant that on less humid days, peak pollen availability occurred later in the day. This finding is unusual as previous studies have found dehiscence in acacia species to be later on more humid days (Stone et al. 1998, Raine 2001). In these studies the positive effect could be explained by a threshold relative humidity that was necessary before dehiscence could begin, however it was not possible to explain the findings for *S. brevispica* in this study in the same way. Although the relationships were not significant, *V. drepanolobium*, *V. etbaica*, *V. gerrardii* and *S. mellifera* also had negative regression slopes between relative humidity and the timing of maximum pollen availability (Fig. 4.19). Only *V. nilotica* had a positive regression slope.

Table 4.6 Results of regression analyses between mean relative humidity over various two hour periods and the time of maximum pollen availability for *S. brevispica*.

| | degrees of freedom | F | p | significance with p=0.0012 |
|---|---|---|---|---|
| 7.00-9.00 | 6 | 4.71 | 0.082 | NS |
| 8.00-10.00 | 8 | 11.23 | 0.012 | NS |
| 9.00-11.00 | 10 | 0.48 | 0.505 | NS |
| 10.00-12.00 | 10 | 14.38 | 0.004 | NS |
| 11.00-13.00 | 10 | 22.51 | 0.001 | * |
| 12.00-14.00 | 9 | 21.96 | 0.001 | * |
| 13.00-15.00 | 10 | 9.88 | 0.012 | NS |
| 14.00-16.00 | 10 | 5.86 | 0.039 | NS |

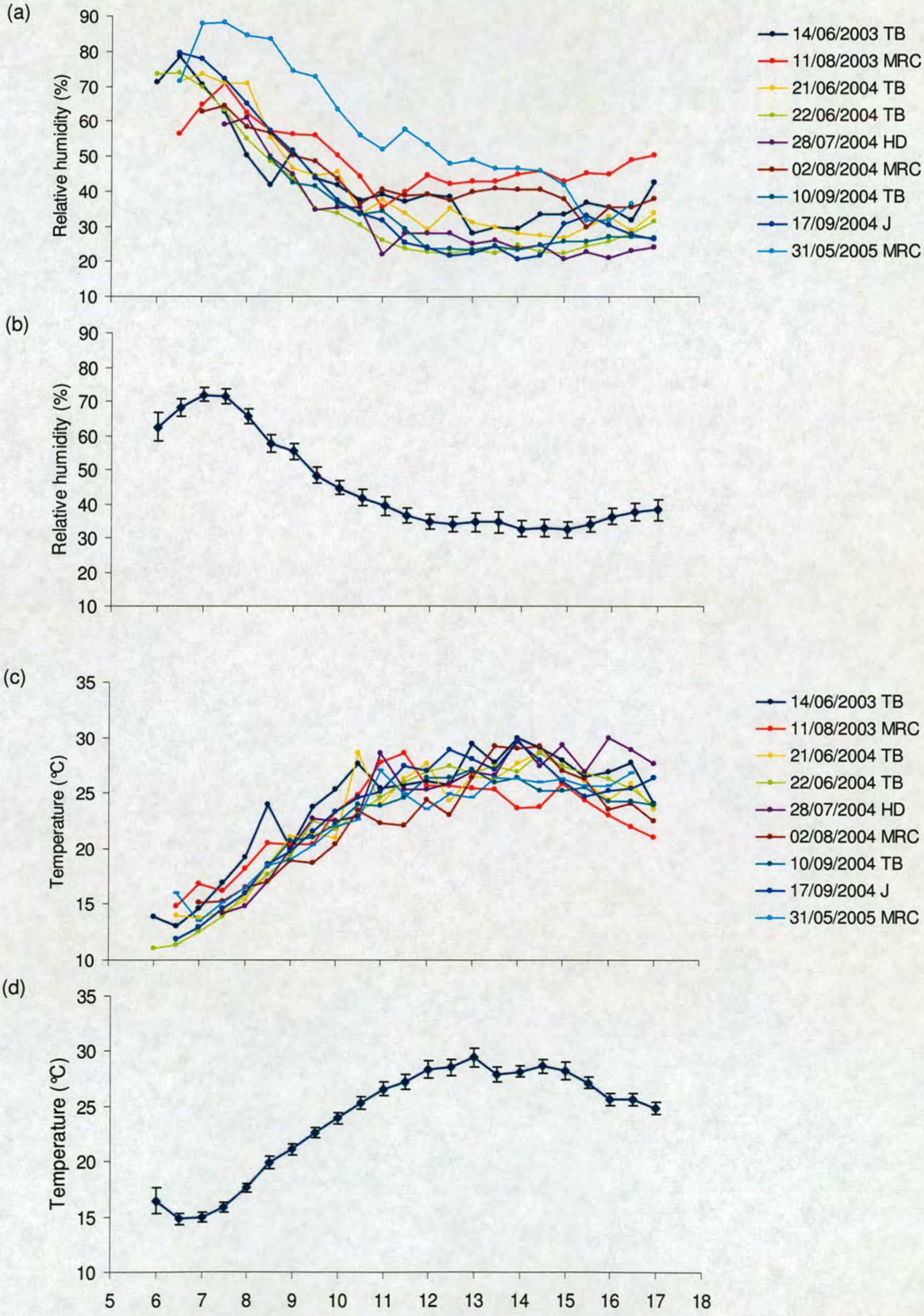
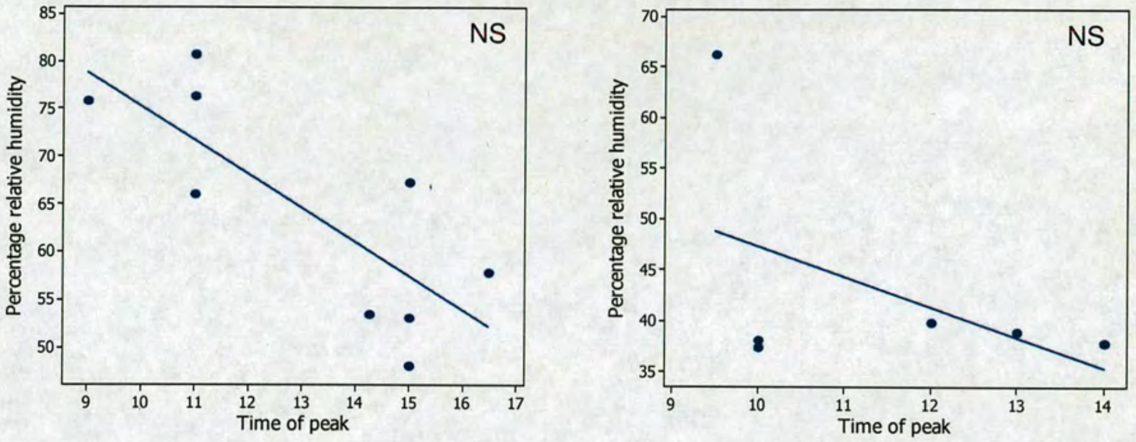
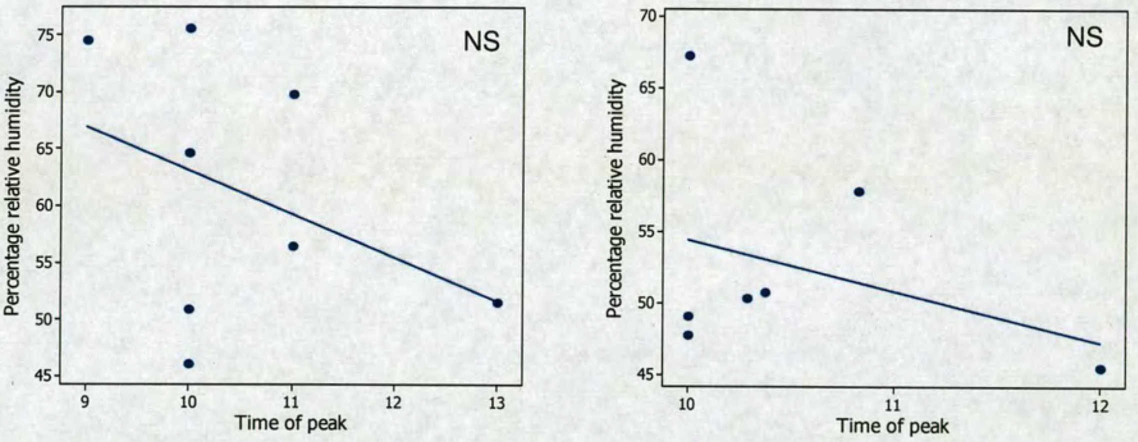


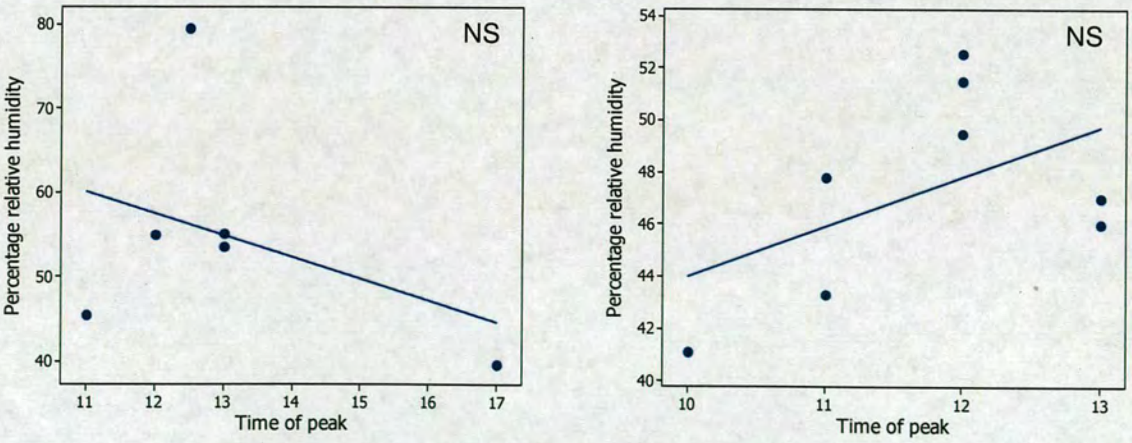
Figure 4.18 Relative humidity (%) and temperature (℃) on sampling days. (a) examples of daily relative humidity patterns, (b) mean relative humidity across all sampling days (± 1SE), (c) examples of daily temperature patterns, (d) mean temperature across all sampling days (± 1SE).


(a) *S. brevispica*

(b) *V. drepanolobium*


(c) *V. etbaica*

(d) *V. gerrardii*


(e) *S. mellifera*

(f) *V. nilotica*

Figure 4.19 Relationship between the time of maximum pollen availability and mean relative humidity between 8.00 and 10.00 for *S. brevispica*, *V. drepanolobium*, *V. etbaica*, *V. gerrardii*, *S. mellifera* and *V. nilotica*. The results of regression analyses are shown in the top right hand corner of each graph.

### 4.3.3 Do differences in the daily timing of pollen release between species provide evidence of competitive displacement?

Regular spacing of pollen availability peaks among species in daily time is compatible with character displacement due to competition for pollinators. Williams' (1995) *V* statistic was used to test whether the pollen availability peaks of the most frequently co-flowering species (*S. brevispica*, *V. drepanolobium*, *V. gerrardii*, *V. nilotica* and *V. seyal)* were regularly spaced at individual sites, and for the overall data across Mpala, between (i) dawn and dusk (6.00-18.00) and (ii) the first and last peaks at each site.

*(a) At individual sites*

Analyses could only be conducted for species at Junction and Turkana Boma since too few of these species were present or sampled at the other sites.

*(i) Turkana Boma*

All five species that frequently co-flowered were sampled at Turkana Boma. Three species had mean pollen availability peaks at 10.00 (*V. drepanolobium*, *V. gerrardii* and *V. seyal*), *V. nilotica* peaked at 11.00 and *S. brevispica* peaked at 15.00 (Table 4.5). Calculation of the *V* statistic for any combination of three or more of these species found that no species combinations were significantly regularly spaced between either dawn and dusk or the first and last species' peaks.

*(ii) Junction*

All frequently co-flowering species except *V. seyal* were sampled at Junction. Mean pollen availability peaks were at 10.00, 12.00, 14.00 and 15.00 for *V. gerrardii*, *V. drepanolobium*, *V. nilotica* and *S. brevispica* respectively (Table 4.5). The peaks of these four species were not significantly regularly spaced between either dawn and dusk or the first and last species' peaks. Calculation of the *V* statistic for combinations of three of these species found that only one species combination (*V. gerrardii*, *V. drepanolobium* and *V. nilotica*) was significantly regularly spaced between the first and last species' peaks ($V$=0.00, $p<0.00001$), but not between dawn and dusk. *V* was calculated as 0 since calculated mean pollen availability peaks for these species were exactly two hours apart.

*(b) Overall at Mpala*

The overall pollen availability patterns for each species were calculated as the mean across all sites (Fig. 4.20). The time of the pollen availability peaks across Mpala are shown for all species in Table 4.5. Calculation of the *V* statistic for any combination of three to five of the most frequently co-flowering acacia species (*S. brevispica*, *V. drepanolobium*, *V. gerrardii*, *V. nilotica* and *V. seyal*) found that no species combinations were significantly regularly spaced between either dawn and dusk or the first and last species' peaks.

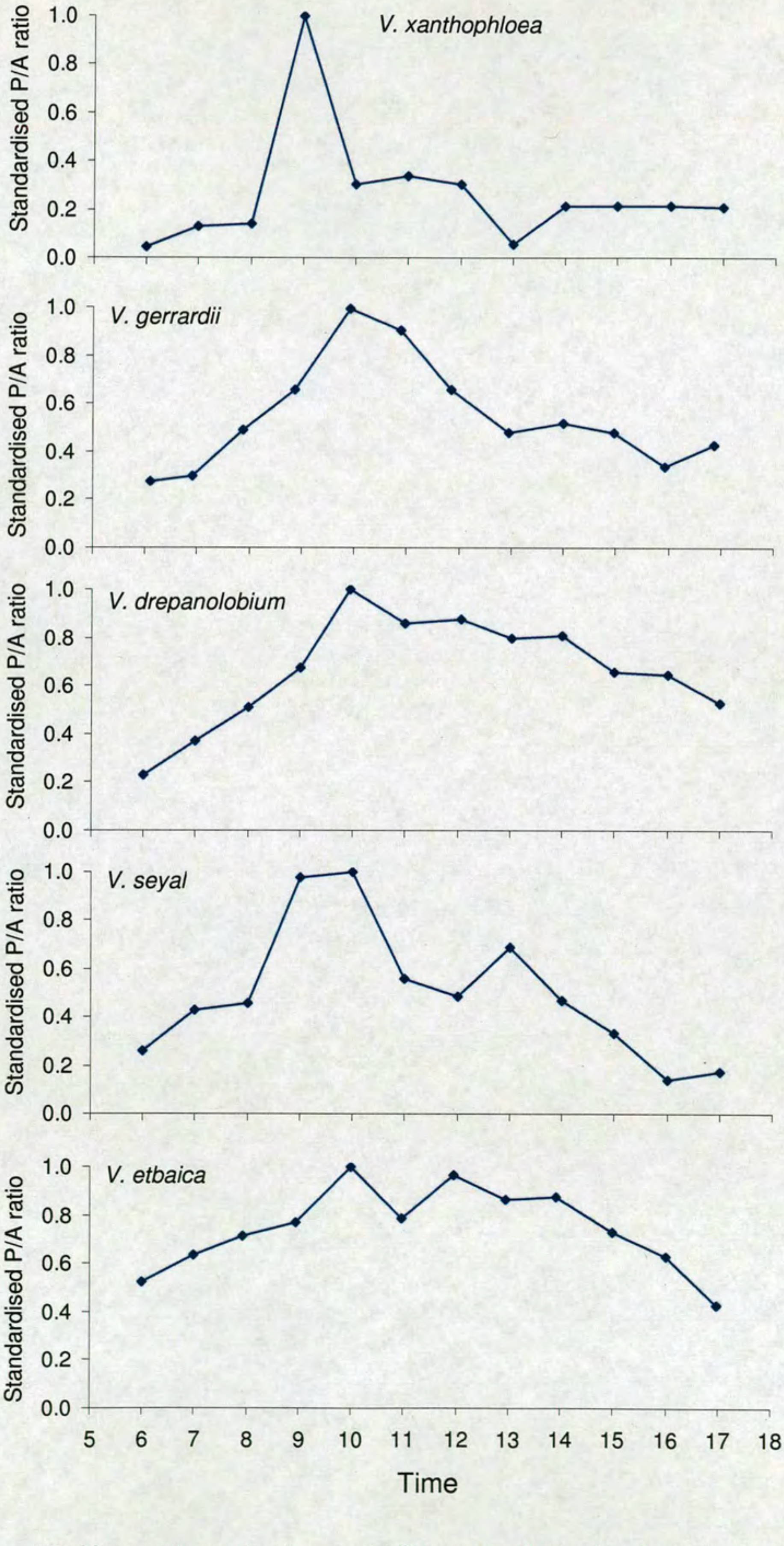


Figure 4.20 Mean patterns of pollen availability across all sites for all acacia species at Mpala. Species are ordered by time of maximum pollen availability, starting with the earliest.

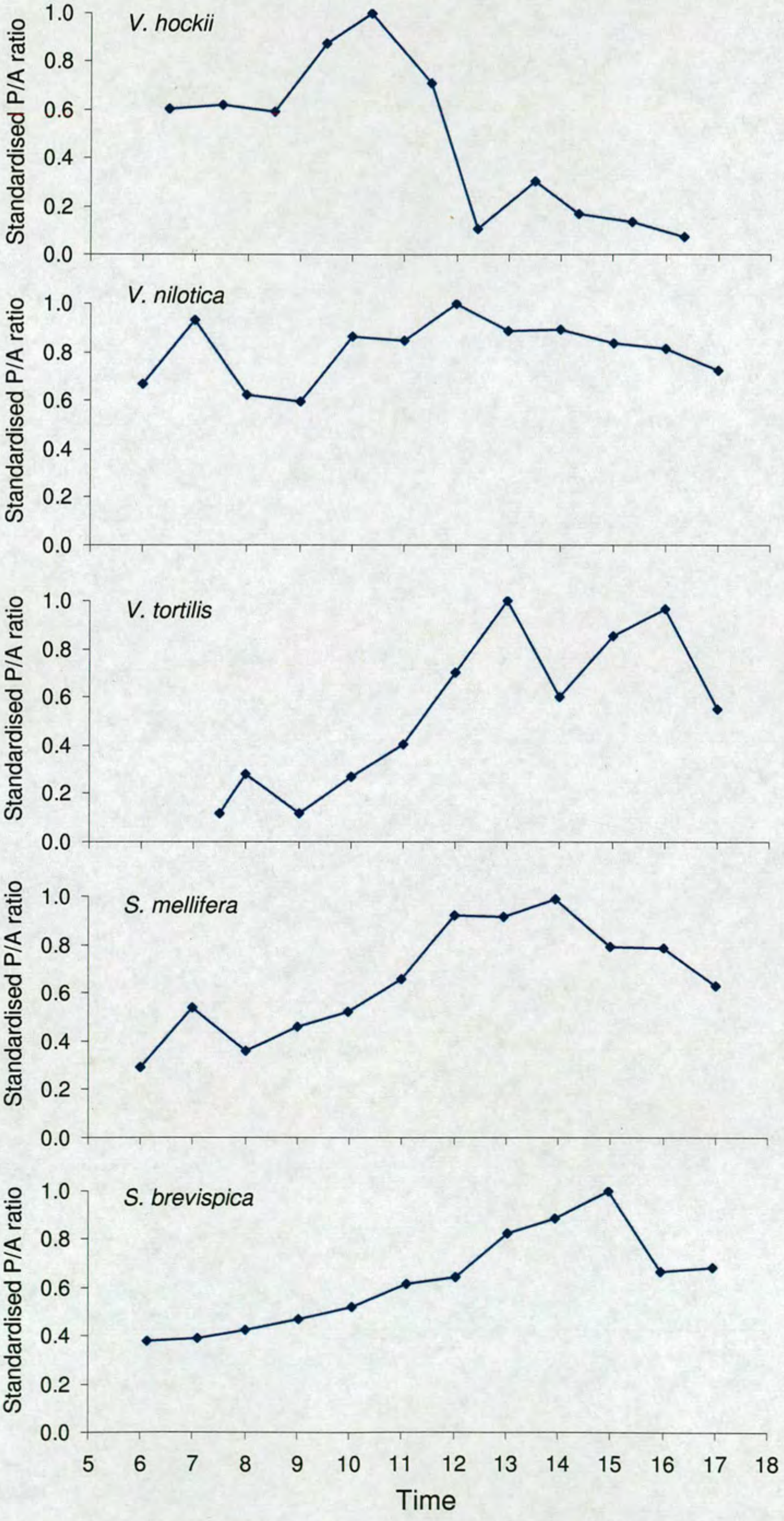


Figure 4.20 (cont.) Mean patterns of pollen availability across all sites for all acacia species at Mpala. Species are ordered by time of maximum pollen availability, starting with the earliest.

## 4.4 Discussion

### 4.4.1 Do acacia species show intraspecific synchrony in the daily timing of dehiscence?

Most acacia species at Mpala showed little intraspecific synchrony in the timing of maximum pollen availability. *Vachellia gerrardii* showed the most consistent patterns within and across sampling days and across sites (Figs. 4.5, 4.15), although pollen availability peaks of individual trees sampled on a single day were never significantly aggregated between dawn and dusk (Section 4.3.1a). *Vachellia tortilis* and *V. xanthophloea* each had similar pollen availability patterns between trees, and *V. seyal* had similar pollen availability patterns between trees and sampling days; however these species were sampled on only one or two days each at a single site (Figs. 4.8, 4.9, 4.12). *Senegalia brevispica*, *V. drepanolobium*, *V. etbaica*, *S. mellifera* and *V. nilotica* all showed considerable variation in pollen availability patterns among trees sampled on the same day, among sampling days for individual trees and across sampling days at each site (Figs. 4.2-4.4, 4.6-4.7, 4.10-4.12, 4.14, 4.16-4.17).

*Senegalia brevispica*, *V. drepanolobium*, *V. etbaica*, *S. mellifera* and *V. nilotica* trees also displayed unusual patterns of pollen availability (Figs. 4.2, 4.3, 4.4, 4.6, 4.7). Several trees had multiple pollen availability peaks on a single day. Some of these incorporated peaks at the start or end of the day, although occasionally several peaks were observed within a sampling day. The expected pattern of pollen availability throughout the day is for the pollen to anther ratio to increase as dehiscence takes place, and to subsequently decrease as pollen is removed by floral visitors (Fig. 4.1). If pollen is released and removed within a short time window we expect a single clear peak of pollen availability, as demonstrated by most of the *V. gerrardii* trees sampled; however if dehiscence and pollen removal by visitors take place over a longer timescale, or visitation is patchily distributed across flower heads, then several peaks might occur.

Several trees had pollen availability peaks early in the morning (6.00-8.00). This could have been because dehiscence occurred earlier than sampling began; however in some trees pollen availability subsequently decreased and then increased to another peak later in the day. If fresh looking flower heads that had dehisced on the previous day had retained pollen and been sampled early the next morning, this could explain high pollen to anther ratios early in the morning followed by later dehiscence peaks. In this scenario the flower heads due to open and dehisce on that day could remain closed at the start of sampling and only open and dehisce later in the day. This theory is supported to some extent by the fact that some trees still had relatively high pollen to anther ratios at the end of sampling days, which suggests that visitors had not removed all available pollen on flower heads. Further sampling is required to reveal whether or not these complex patterns are genuine or the result of inadequate sampling. The sampling of more flower heads at each time, and careful marking of flower heads on each day, could help to identify which pollen availability peaks are due to dehiscence on that day and which are from older flower heads.

The results of this study contrast with the high intraspecific synchrony shown by acacia species in a Tanzanian community in a similar habitat (Stone et al. 1996, 1998). At this site (Mkomazi) co-flowering species each dehisced during a short daily time window. Four of the Tanzanian acacias were present at Mpala (*S. brevispica*, *V. drepanolobium*, *V. nilotica* and *V. tortilis*). Although most of the Mpala acacias showed a lot of intraspecific variation in the timing of dehiscence, the mean pollen availability peaks calculated across all days were similar among sites in some species (Table 4.5). Furthermore some of these corresponded to those for the same species at Mkomazi. At Mpala, the overall data indicate that *S. brevispica* has a pollen availability peak at 15.00 (Fig. 4.20), which corresponds to the time of the pollen availability peak at Mkomazi (Table 4.7). Similarly the overall pollen availability peak for *V. drepanolobium* occurred at a similar time at both locations (Table 4.7). At Mkomazi, pollen availability in *V. nilotica* peaked between 6.00 and 7.00 (Table 4.7). Although a peak was observed at the same time for this species at Mpala, dehiscence patterns were extremely variable and an additional peak occurred at 12.00 (Fig. 4.20).

Table 4.7 Times of overall pollen availability peaks for species present at both Mkomazi and Mpala.

| | Mkomazi | Mpala |
|---|---|---|
| *S. brevispica* | 15.00-16.00 | 15.00 |
| *V. drepanolobium* | 10.00-12.00 | 10.00 |
| *V. etbaica* | not sampled | 10.00 |
| *V. nilotica* | 6.00-7.00 | 12.00* |
| *V. tortilis* | 7.50-9.00 | 13.00 |

* There was also a slightly smaller peak at 7.00

### 4.4.2 Assessment of data quality

Sampling in this study was designed to target multiple flower heads for multiple acacia species at each sampling point. Sampling effort was limited by manpower, and by the number of flower heads available on a tree. The time taken to score slides also limited the number of trees that could be sampled; slides for a single tree with four flower heads sampled hourly between 6.00 and 17.00 took up to eight hours to score.

By sampling every hour, I hoped to capture most of the daily variation in pollen availability. However, if flower heads that released pollen and were harvested during a short time window were included in samples, the maximum daily dehiscence peak could have been missed, or the strength of the peak could be lower relative to consecutive sampling times. Flower head removal for trees with a low density of flower heads could also have affected visitation later in the day due to a decrease in the amount of floral reward on that tree available to visitors and resulted in relatively high pollen to anther ratios later in the day for remaining unvisited flower heads.

The unusual patterns of pollen availability observed for some species (i.e. multiple peaks and high ratios at the start and end of sampling days) could have been due to sampling error. As described above, sampling of flower heads from the previous day could have resulted in higher pollen to anther ratios early in the day. More detailed studies over several days might reveal whether the patterns of pollen availability observed in this study were real, or due to sampling error. This was carried out for multiple *V. nilotica* trees at Turkana Boma in 2005 (unpublished results). This study found that two cohorts of flower heads with pollen available were present on a single tree on a single day. The first cohort dehisced at approximately midday on day 1 and had pollen remaining at the end of the day. Pollen to anther ratios for these flower heads remained high at the start of day 2 but decreased rapidly throughout the morning, and were much lower by midday (see Fig. 4.21). The new flower heads opening on day 2 dehisced at approximately midday and still had relatively high pollen to anther ratios at the end of day 2.

The consequences of combining these two cohorts of flower heads in a single sample are that high pollen to anther ratios will be found at the start and end of sampling days, accompanied by peaks at approximately midday. This pattern was found for many of the trees sampled at both Turkana Boma and MRC. If the different cohorts of flower heads could be taken into account when examining the patterns of pollen availability for *V. nilotica* found in this study, we might find that flower heads opening on the day the tree was sampled all dehisced synchronously within a 2-3 hour time window between approximately 11.00 and 14.00. Detailed examination of pollen availability in this way could reveal similar patterns for other species with complex dehiscence patterns, e.g. *S. brevispica* and *V. etbaica*.

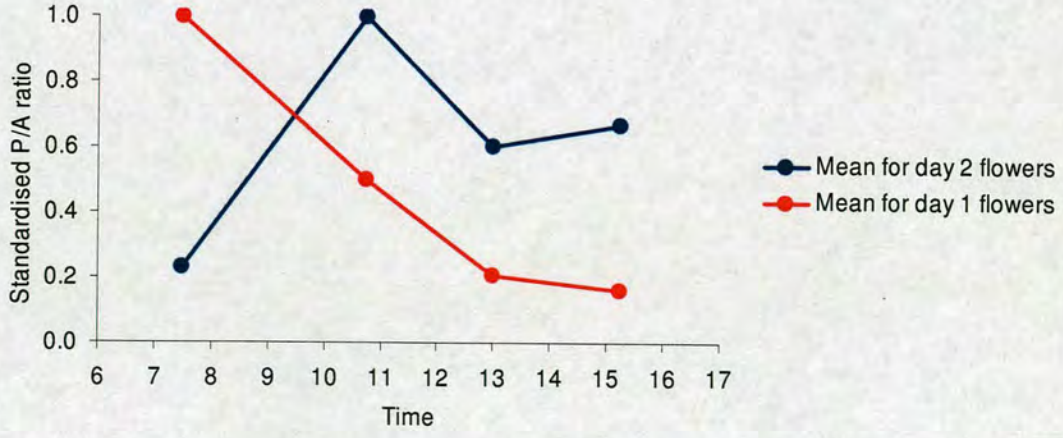


Figure 4.21 Mean pollen to anther ratios calculated across six *V. nilotica* trees sampled on 1st July 2005. Day 1 flowers are those that opened and dehisced on 30th June 2005 and day 2 flower heads are those that opened and dehisced on 1st July.

### 4.4.3 Can variation in the timing of dehiscence within species be explained by variation in relative humidity?

Studies of different plant taxa have found that dehiscence is linked to relative humidity in many species, with dehiscence occurring at lower relative humidities and high relative humidities inhibiting dehiscence (Yates and Sparks 1993, Lisci et al. 1994, Bianchini and Pacini 1996, Gradziel and Weinbaum 1999, Kozlowski and Pallardy 2002). Anther opening is considered to be a process involving tissue desiccation (reviewed in Garcia et al. 2006) and changes in relative humidity have been suggested as a causal mechanism triggering anther dehiscence through differential rates of tissue drying within the anther wall (Keijzer 1987, Bonner and Dickenson 1989, 1990, Keijzer et al. 1999).

Previous studies of acacias have shown that the variation in timing of dehiscence between days in some African and Mexican species was linked to relative humidity (Stone et al. 1998, Raine 2001). In these studies dehiscence occurred when decreasing relative humidity reached a minimum threshold level.

Variation in the timing of dehiscence was not explained by variation in relative humidity for most acacia species at Mpala (Fig. 4.18). Only *S. brevispica* had a significant relationship, this being a negative correlation between the timing of dehiscence and relative humidity (i.e. lower relative humidity meant pollen availability peaks occurred later in the day). However this result conflicts with the findings for other acacias (Stone et al. 1998, Raine 2001) and is difficult to explain, given what is known about the timing of dehiscence in relation to relative humidity for other plant taxa.

I suggest that this relationship may be coincidental, especially given the lack of a relationship between relative humidity and maximum pollen availability for other acacias at Mpala. The time of maximum pollen availability varied between 8.00 and 17.00 in *S. brevispica* individuals and it is unlikely that this amount of variation is due to variation in relative humidity.

### 4.4.4 Do differences in patterns of pollen availability between acacia species provide evidence of competitive displacement?

Assuming that the data collected in this study are correct, there is little evidence to suggest the divergence of dehiscence in daily time among the Mpala acacia species. Few species demonstrated intraspecific synchrony in the timing of dehiscence and the pollen availability peaks for groups of frequently co-flowering species were not significantly regularly spaced in daily time for almost all species combinations tested at Turkana Boma, Junction or the overall data across Mpala. In contrast to expectations of partitioning, pollen availability peaks calculated across all data for each species occurred at the same time (10.00) for five species, three of which frequently co-flowered with other acacias: *V. drepanolobium*, *V. etbaica*, *V. gerrardii* *V. hockii* and *V. seyal* (Table 4.5).

At Junction, the peaks for three co-flowering species (*V. gerrardii*, *V. drepanolobium* and *V. nilotica*) were significantly regularly spaced between the first and last species, although not between dawn and dusk. However, the times of the peaks differed from those of the same species at other sites, and only one *V. nilotica* tree was sampled. Furthermore *S. brevispica* and *V. seyal* also frequently co-flowered with these species. Whilst the peak pollen availability for *S. brevispica* occurred at a different time (15.00) this time was not incorporated into a significantly regularly spaced pattern of species' peaks, and *V. seyal* was not sampled at Junction. Considering all of these factors, and that the time of the pollen availability peak for *V. drepanolobium* was highly variable between individuals, I consider the support for competitive displacement of dehiscence in daily time at this site to be weak.

These findings contrast with those of Stone et al. (1996, 1998) who found that the pollen availability peaks of six co-flowering acacias in a Tanzanian acacia community were significantly regularly spaced in daily time. *Senegalia brevispica*, *S. bussei*, *V. nilotica*, *S. senegal*, *V. tortilis* and *V. zanzibarica* were regularly spaced between dawn and dusk, as well as between the first and last species, and visits by shared pollinators closely tracked the pollen availability peaks among species. This showed evidence of pollinator partitioning in daily time through competitive displacement of dehiscence in daily time as a response to competition for shared pollinators. In most species dehiscence occurred at a specific relative humidity which suggests that daily cycles of relative humidity could structure interspecific patterns of dehiscence. The observed daily structure among 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, such as pod dehiscence (Grant 1996, Bailey et al. 1997).

Although three of these six acacias were present at Mpala (*S. brevispica*, *V. nilotica* and *V. tortilis*), no evidence was found to suggest that divergence had occurred in the timing of dehiscence among co-flowering acacia species due to competitive displacement. In addition, whilst the timing of dehiscence was highly synchronous among individuals for both *V. nilotica* and *S. brevispica* at the Tanzanian site (Mkomazi), the timing of dehiscence was extremely variable for the same two species at Mpala (Fig. 4.20). Furthermore, the acacias at Mpala did not dehisce at specific relative humidities. In comparison to the Mkomazi acacias, the Mpala acacias lacked both structure in the timing of dehiscence amongst co-flowering species and a link between dehiscence and relative humidity.

The lack of evidence for competitive displacement in the timing of dehiscence among the Mpala acacias could be due to problems with sampling (see Section 4.4.2). However, if the data are representative of the patterns at Mpala, this could be explained by lower intensities of competition for pollinators due to extended flowering seasons (see Chapter 3). Species with short flowering seasons in the highly seasonal climate of Mkomazi flowered over longer timespans at Mpala (e.g. *V. nilotica*, *V. drepanolobium*, *S. brevispica*). Consequently acacias with simultaneous flowering peaks after the main (autumn) rains at Mkomazi competed for shared pollinators with several other species in a relatively short seasonal time window. In contrast, flowering peaks were not simultaneous among multiple co-flowering species at Mpala which could result in less intense competition for pollinators and mean that species experience fewer negative effects if pollinators are shared. In addition, different sets of species co-flowered at different times at Mpala, which could mean that no consistent selective pressure exists at this site to drive competitive displacement.

Results from other studies of acacias indicate that when competition for pollinators is less intense, there is less synchrony in the timing of dehiscence among conspecific individuals. At Mkomazi, acacias that flowered during the dry season, and shared flowering seasons with few other acacias, showed less intraspecific synchrony than those co-flowering with multiple acacia species (Stone et al. 1998). In Mexico, Raine (2001) observed that when *V. macrancantha* and *S. angustissima* grew in sympatry, both showed high levels of intraspecific synchrony as well as interspecific divergence in the timing of dehiscence. However in locations where *V. macracantha* grew without *S. angustissima*, trees showed far less synchrony in the timing of dehiscence. In a study of temperate Australian acacias, Prescott (2005) showed that seven sympatric species all dehisced at similar times of day, with dehiscence beginning early in the morning and continuing into the late morning or early afternoon. The flowering seasons of acacias in this community were to a large extent separated in seasonal time, although flowering overlapped among some species, and, whilst species shared pollinators, segregation in seasonal time could have reduced intense competition for pollination.

Given the differences between acacia assemblages studied in two similar habitats (Mpala and Mkomazi) it would be interesting to examine the extent to which other acacia assemblages in the same region demonstrate daily structure among co-flowering species. Can the differences between Mpala and Mkomazi be solely attributed to extended seasonal flowering phenologies or does daily structure in the timing of dehiscence among co-flowering species depend on the species involved? Although dehiscence was not regularly spaced in daily time among co-flowering acacias at Mpala, there is some evidence to suggest that individual species dehisce at particular times. It would be interesting to know if this an artefact of dehiscence times for these species in more seasonal habitats, or whether dehiscence at a particular time of the day, confers some reproductive advantage for co-flowering species.

# Chapter 5. Daily patterns of visitation to acacia flower heads

## Summary

Floral visitor assemblages and patterns of visitation in daily time were examined for seven acacia species at Mpala: *S. brevispica*, *V. drepanolobium*, *V. etbaica*, *V. gerrardii*, *V. hockii*, *S. mellifera* and *V. nilotica*. The visitor assemblages of *V. drepanolobium*, *V. etbaica*, *S. mellifera* and *V. nilotica* were dominated by bees, whereas those of *S. brevispica*, *V. gerrardii* and *V. hockii* were a mixture of bees and flies. Comparisons of visitor assemblages revealed that *S. brevispica* and *V. gerrardii* had the most similar visitor assemblages with flies and bees grouped to family level. Both species were visited by megachilid bees, calliphorid flies and syrphid flies. The visitor assemblage for *V. hockii* was most similar to those of *S. brevispica* and *V. gerrardii*. The visitor assemblages for *V. drepanolobium*, *V. etbaica*, *S. mellifera* and *V. nilotica* were very similar at a low taxonomic resolution but far less similar when flies and bees were considered at family level. This suggests that whilst bees dominate visits in these four acacias, the particular bee visitor species differ between species. Daily visitation patterns for each species varied across days and overlapped in daily time with other acacias. High visitation rates corresponded to high levels of pollen availability, with bees tracking pollen more often than flies.

The identification of visitors captured on flower heads over a two year period allowed comparisons of visitors at the species level. These data revealed a much wider diversity of visitor species for the six acacias examined in this way (*S. brevispica*, *V. drepanolobium*, *V. etbaica*, *V. gerrardii*, *S. mellifera* and *V. nilotica*). Ninety-one visitor species were recorded on multiple acacias. Four bees, *Apis mellifera*, *Macrogalea candida*, *Braunsapis ?bouyssoui* (all Apidae) and a species of *Pseudapis* (Halictidae) visited flower heads of all six acacias.

Acacias at Mpala have the potential to compete for pollinators since visitor species are shared and visitation patterns overlap in daily time. However the importance of these shared visitors as pollinators for each acacia species is unknown.

## 5.1 Introduction

In Chapter 4, I examined the daily patterns of pollen availability for the Mpala acacias. Although there was variation in the timing of pollen release across acacia species, I found no evidence for divergence in the daily timing of dehiscence among regularly co-flowering species. Pollen availability peaks for *S. brevispica*, *V. etbaica*, *V. gerrardii*, *V. nilotica* and *V. seyal*, the acacia species that most frequently co-flowered at Mpala, were not significantly regularly spaced in daily time.

If accurate, these results suggest that co-flowering acacias either do not compete for pollinator visits, or that competition for pollinators has little impact on the reproduction of co-flowering species. This in turn could be because there is little overlap among the pollinator assemblages of co-flowering acacias at Mpala, or that visitation rates by shared pollinators are sufficient for competition to be inconsequential. It must be borne in mind however that even if shared pollinators are abundant, expected negative effects of interspecific pollen transfer could still drive partitioning of shared pollinator visits.

In this chapter I examine floral visitor assemblages and daily patterns of visitation to flower heads for acacia species at Mpala. This allows the identification and quantification of activity in shared visitors. Daily patterns of visitation are then compared between species to examine whether visits by shared pollinators are structured in daily time among acacia species. Finally, I compare daily visitation patterns to the patterns of pollen availability shown in Chapter 4. Visitation patterns that closely track patterns of pollen availability would be compatible with structuring of pollinator activity as a result of pollen release in daily time. In this chapter I first summarise the main groups of visitors to acacia flower heads and describe daily patterns of visitation found in previous studies. I review the evidence for pollinator partitioning in daily time in groups of acacias found to date. I then address the following specific questions for the acacias at Mpala:

1. Do individual acacia species have characteristic floral visitor assemblages?

2. How variable are the floral visitor assemblages for individual acacia species?

3. Do acacia species share floral visitors and do their visits represent a significant proportion of all visits?

4. Do daily patterns of visitation vary within and between acacia species?

5. Do patterns of visitation track patterns of pollen availability in each acacia species?

### 5.1.1 Visitors to acacia flower heads

The open structure of acacia flower heads makes them accessible to a wide range of flower visitors. The visitor assemblages associated with different acacia species are determined by the local pool of potential visitors and the floral resources available. Acacias that offer nectar in addition to pollen are generally visited by more diverse insect assemblages than those offering solely pollen (Stone et al. 1998). Acacia visitors can generally be divided into three groups: (i) specialist pollen and flower feeders (bees, beetles and many of the true flies), (ii) specialist nectar feeders (birds, butterflies and bee flies (Bombyliidae)) and (iii) opportunist foragers (some fly taxa, ants and wasps).

Not all visitors to acacia flower heads will be effective pollinators. The efficacy of visitor taxa as pollinators of each acacia species will be determined by several factors including (i) the frequency with which they visit flower heads, (ii) the level of fidelity to flower heads of the same species (known as floral constancy) (iii) the amount of pollen carried that is available for transfer to subsequent flower heads and (iv) the extent to which they move pollen between flower heads on different trees.

The most frequent visitors to acacias are usually bees, along with syrphid and calliphorid flies (Stone et al. 1996, 1998, Raine 2001, Stone et al. 2003). Bees are the only visitors to acacia flower heads that actively collect, externally store and transport large amounts of pollen. Since bees collect pollen in order to provision their larvae they collect far more pollen than they require individually. In contrast, almost all other visitors collect pollen whilst engaged in other activities such as nectar foraging, feeding on pollen *in situ*, eating the flowers themselves (flower predation) or searching for prey. Floral constancy refers to the tendency of a pollinator to restrict its visits to flowers of a single species (Waser 1986). Evidence for high levels of floral constancy in bees has been found for honeybees (Grant 1950), bumblebees (Heinrich 1976, Free 1970, Yang et al. 2007) and stingless social bees (see Heard 1999, White et al. 2001), as well as solitary species (Ne'eman et al. 2006). The effectiveness of flies in pollinating acacias depends on their behaviour and patterns of movement among trees, which vary between taxa. Hoverflies (Syrphidae) are pollen feeders that move rapidly among flower heads and between trees (G. N. Stone, unpubl. data) and so are potentially important pollen vectors. Syrphids have been shown to demonstrate high levels of floral constancy (Goulson and Wright 1998). Other fly taxa, such as calliphorid flies, often remain on individual flower heads for long periods of time (Stone et al. 2003). Wasps, ants, beetles and butterflies all visit acacia flower heads but usually do so less frequently (Stone et al. 1998, 2003, Raine 2001).

Floral visitors for acacias in the genera *Vachellia* and *Senegalia* have been studied in Tanzania (Stone et al. 1996, 1998), Kenya (Tybirk 1988, 1989, 1993), Senegal (Tybirk 1993), Mexico (Raine 2001) and India (Tandon et al. 2001). The visitors to acacia heads found in these studies are outlined below. Much of the following is summarised from Stone et al. (2003).

### *(a) Bees (Hymenoptera: Apoidea)*

All acacia species that have been studied are visited by bees. A wide variety of bee species have been recorded visiting acacia flower heads including social apid bees and solitary bees in the Apidae, Colletidae, Megachilidae and Halictidae (Stone et al. 2003). Honeybees (several species in the genus *Apis*) are important pollinators where they are native in Africa and South-east Asia, and in the Americas and Australia, where they are introduced (Tandon et al. 2001, Stone et al. 2003).

Raine (2001) observed a wide diversity of native bee visitors to acacia flower heads in Mexico. These included social stingless bees in the genera *Scaptotrigona* (Apidae) and *Trigona* (Apidae), and solitary bees in the genera *Xylocopa* (Apidae), *Hylaeus* (Colletidae), *Megachile* (Megachilidae), *Augochloropsis* (Halictidae) and *Lasioglossum* (Halictidae).

Bees in the genus *Megachile* are also frequent visitors to acacia flower heads in Africa (Tybirk 1989, 1993, Stone et al. 1996, 1998). Stone et al. (2003) suggest that *Megachile* could be specialist pollen collectors of mimosoids with densely packed flower heads, such as acacias, because of their behaviour when harvesting pollen. These bees somersault around individual flower heads, skimming rapidly over exposed anthers and can therefore collect polyads more rapidly than more generalist foragers such as honeybees. Other frequently observed bee visitors to African acacias were large apid bees in the genera *Xylocopa* (carpenter bees), *Anthophora* and *Amegilla*, honeybees (*Apis mellifera*) and halictid bees in the genera *Nomia* and *Lipotriches* (Tybirk 1989, 1993, Stone et al. 1998). Only one colletid bee species, visiting *S. senegal*, was recorded during these studies (Tybirk 1993).

### *(b) Wasps (Hymenoptera)*

Wasps visit acacia flower heads for nectar or in search of prey (Stone et al. 2003). Many wasp visitors are predatory (e.g. Eumenidae, Sphecidae, Pompilidae) or parasitic (e.g. Chrysididae, Scoliidae, Ichneumonidae) (Tybirk 1993, Raine 2001, Tandon et al. 2001). Parasitic and carnivorous wasps usually obtain proteins from hosts or prey and are not known to feed on pollen, but some forage for nectar as an energy source (Scholtz and Holm 1986). Stone et al. (1996, 1998) found larger proportions of wasp visitors on nectar-producing acacias, although species that didn't produce nectar were also visited by wasps.

### *(c) Ants (Hymenoptera: family Formicidae)*

Raine (2001) recorded ant visitors on flower heads in Mexico, although these formed a small proportion of total visits. Ants are thought to be opportunist visitors to acacia flower heads, foraging mainly for nectar or prey items (Stone et al. 2003), and are considered to be ineffective pollinators since movement between trees is likely to be limited. Furthermore ant secretions have been found to reduce pollen viability (Beattie et al. 1985, Wagner 2000).

Ant-plant mutualisms occur in many acacia species in the Americas and Africa, including *V. drepanolobium* at Mpala. Ants reside on trees in modified thorns (pseudogalls) and guard the trees against attack by herbivores and encroachment by vegetation (e.g. Janzen 1966, 1967a, Hocking 1970, Young et al. 1997). Aggressive ant-guards could potentially deter pollinators, however studies have shown that young acacia flower heads produce chemicals that repel ant guards during times at which pollinators visit (Willmer and Stone 1997a, Raine et al. 2001).

### *(d) Flies (Diptera)*

Acacia flower heads are visited by a wide diversity of true flies, most of which are pollen feeders (Gilbert 1981, Tybirk 1993, Stone et al. 1999a, 2003). Syrphids feed on pollen and have been observed visiting acacia flower heads in Africa (Tybirk 1989, 1993, Stone et al. 1996, 1998) and Mexico (Raine 2001). Other flies found on acacias include species in the families Calliphoridae, Muscidae, Tachinidae and Sarcophagidae (Tybirk 1993, Stone et al. 1999a). These taxa feed on pollen and/or floral exudates on acacia flower heads. The latter food source is inferred because flies have been seen to feed before dehiscence on the flower heads in questions had occurred (G. N. Stone, pers. comm.). Certainly, these fly taxa are known to feed on both floral nectar and pollen in other plant species (Proctor et al. 1996). Of these, only calliphorid flies have been observed in large numbers on acacias, and individuals often remain on individual flower heads for long periods of time (Stone et al. 2003). Other fly taxa observed on acacia flower heads include nectar-feeding beeflies (Bombyliidae) and predatory flies, such as Asilidae (Tybirk 1993, Stone et al. 1999a, Raine 2001). Most studies have found flies to be less frequent visitors to acacia flower heads than bees, although the Mexican species *V. farnesiana* received more visits from flies than any other visitor group (Raine 2001).

### *(e) Butterflies (Lepidoptera)*

Butterflies are obligate nectar feeders and are abundant only on acacias that secrete nectar (Stone et al. 2003). In most studies they are responsible for a small proportion of visits to acacia flower heads and carry relatively low quantities of polyads on their bodies (Tandon et al. 2001, Raine 2001). Species observed on acacias in Tanzania, Senegal and India belonged to a variety of families including Lycaenidae, Nymphalidae, Papilionidae and Pieridae (Tybirk 1993, Stone et al. 1999a, Tandon et al. 2001).

*(f) Beetles (Coleoptera)*

Beetles have been recorded visiting acacia flower heads in most previous studies (Tybirk 1989, 1993, Stone et al. 1996, 1999a, Raine 2001, Tandon et al. 2001). In Mexico and Senegal, beetle visitors included Chrysomelidae and Scarabaeidae which are often flower predators (Jolivet 1995), although can be effective pollinators for some plant species (Ollerton et al. 2003). Other frequent beetle visitors such as Cantharidae and Coccinellidae are predators (Chinery 1993) that probably visit acacia flower heads in search of prey.

*(g) Vertebrates*

Sunbirds (Nectariniidae) visit nectar producing acacias in both Tanzania and Senegal (Tybirk 1993, Stone et al. 1998). Few other vertebrates have been observed visiting acacia flower heads. Du Toit (1990) proposed that giraffes (*Giraffa camelopardalis*) might be important pollinators of *S. nigrescens* in southern Africa, since they consume large numbers of flower heads. However, a recent study by Fleming et al. (2006) found that giraffes were flower predators, rather than pollinators.

### 5.1.2 Daily temporal patterns of visitation to acacia flower heads

Co-flowering plant species that share pollinators could reduce interspecific competition by structuring pollinator visits in daily time (see Chapter 1, Section 1.1). Evidence for this has been found in groups of co-flowering species in Tanzania (Stone et al. 1996, 1998) and Mexico (Raine 2001). Dominant visitors in these studies were bees, syrphid and calliphorid flies.

In these studies daily patterns of visitation for individual acacia species were largely determined by pollen availability, with overall patterns of visitation to flower heads closely tracking the pollen availability for each species (Stone et al. 1996, 1998, Raine 2001). Where pollen release was structured in daily time among co-flowering acacias, there were sequential peaks of visitation among species. In Tanzania, visits by shared megachilid bee species and honeybees (*Apis mellifera*) closely tracked pollen availability among co-flowering acacia species whose pollen availability peaks were regularly spaced throughout the day. Visits by calliphorid flies also tracked the sequence of dehiscence for these acacias (Stone et al. 1996, 1998). In Mexico, evidence for pollinator partitioning in daily time was found for two co-flowering species, *V. macracantha* and *S. angustissima* (Raine 2001). Partitioning appeared to be driven by differences in the timing of pollen availability.

## 5.2 Methods

### 5.2.1 Study species and sites

I made detailed observations of visitors to flower heads of *S. brevispica*, *V. drepanolobium*, *V. etbaica*, *V. gerrardii*, *S. mellifera* and *V. nilotica* between 21st June and 17th September 2004 and between 20th May and 14th July 2005 (Table 5.1). I was assisted in these observations by Dr G. N. Stone, R. Eraguy and R. Lavin. I have analysed these data alongside data collected for *S. brevispica*, *V. gerrardii*, *V. hockii* and *V. nilotica* in June 1999 by Dr G. N. Stone, Professor P. G. Willmer, Professor A. Schnabel and Dr R. Atkinson (Table 5.2) to examine longer term variation in visitor assemblages between years. The 2004-2005 data set incorporated 47 tree observation days, whilst the 1999 data set incorporated 16 tree observation days (Tables 5.1, 5.2). *Vachellia seyal*, *V. tortilis* and *V. xanthophloea* were not examined for floral visitors as they did not flower during field seasons.

Data were collected for trees at four of the study sites used for the collection of flowering phenology data; Turkana Boma, Mongoose, Junction and High Dam. Observations were carried out for marked trees where possible, however when these were not in flower observations were conducted on nearby trees.

### 5.2.2 Detailed observations of visitor assemblages

Floral visitors were recorded using a similar method to that used by Stone et al. (1996, 1998), Raine (2001) and Prescott (2005). Visitors were recorded for each acacia species by watching the same set of flower heads for 30 minutes of every hour from before the onset of foraging until after it ceased on a given day. Most sampling days started between 6.00 and 8.00 and continued until 17.00. The number of flower heads observed varied depending on the density of flower heads and the amount of flowering for each tree, and was chosen such that they could be easily observed by one person. The number of flower heads observed per tree ranged from nine to 50. During each 30 minute observation period, the number of visits made by each visitor taxon was recorded. A visit was recorded each time a visitor contacted a flower head.

Table 5.1 Number of sampling days for collection of flower head visitation data for each acacia species at each site in 2004 and 2005

| Acacia species | Site | Number of trees | Date |
|---|---|---|---|
| *S. brevispica* | Turkana Boma | 1 | 21st July 2004 |
| | Turkana Boma | 1 | 18th Aug 2004 |
| | Turkana Boma | 1 | 20th Aug 2004 |
| | Turkana Boma | 1 | 6th Sep 2004 |
| | Junction | 1 | 20th May 2005 |
| | Junction | 1 | 24th May 2005 |
| | Junction | 2 | 7th July 2005 |
| | Junction | 2 | 8th July 2005 |
| | High Dam | 1 | 25th May 2005 |
| | High Dam | 2 | 13th June 2005 |
| | High Dam | 1 | 17th June 2005 |
| | High Dam | 2 | 27th June 2005 |
| | **Total** | **16** | |
| *V. drepanolobium* | Turkana Boma | 1 | 13th Sep 2004 |
| | Junction | 1 | 10th Sep 2004 |
| | Junction | 1 | 17th Sep 2004 |
| | **Total** | **3** | |
| *V. etbaica* | Turkana Boma | 1 | 21st Aug 2004 |
| | Turkana Boma | 1 | 27th Aug 2004 |
| | Turkana Boma | 1 | 13th Sep 2004 |
| | **Total** | **3** | |
| *V. gerrardii* | Turkana Boma | 1 | 18th Aug 2004 |
| | Junction | 1 | 30th July 2004 |
| | High Dam | 2 | 28th July 2004 |
| | **Total** | **4** | |
| *S. mellifera* | Turkana Boma | 1 | 6th Sep 2004 |
| *V. nilotica* | Turkana Boma | 1 | 21st June 2004 |
| | Turkana Boma | 1 | 22nd June 2004 |
| | Turkana Boma | 1 | 16th July 2004 |
| | Turkana Boma | 1 | 21st June 2005 |
| | Turkana Boma | 2 | 23rd June 2005 |
| | Turkana Boma | 2 | 24th June 2005 |
| | Turkana Boma | 2 | 28th June 2005 |
| | Turkana Boma | 2 | 29th June 2005 |
| | Turkana Boma | 2 | 30th June 2005 |
| | Turkana Boma | 1 | 12th July 2005 |
| | Turkana Boma | 1 | 13th July 2005 |
| | Turkana Boma | 1 | 14th July 2005 |
| | Junction | 1 | 30th July 2004 |
| | Junction | 1 | 10th Sep 2004 |
| | Junction | 1 | 17th Sep 2004 |
| | **Total** | **20** | |
| **Total tree days** | | **47** | |

Table 5.2 Number of sampling days for collection of flower head visitation data for each acacia species at each site in 1999

| Acacia species | Site | Number of trees | Date |
|---|---|---|---|
| *S. brevispica* | High Dam | 3 | 9th June 1999 |
| *V. gerrardii* | Mongoose | 1 | 6th June 1999 |
| | Mongoose | 2 | 12th June 1999 |
| | High Dam | 2 | 16th June 1999 |
| | High Dam | 1 | 17th June 1999 |
| | Turkana Boma | 1 | 21st June 1999 |
| | **Total** | **7** | |
| *V. hockii* | High Dam | 1 | 17th June 1999 |
| *V. nilotica* | Turkana Boma | 3 | 7th June 1999 |
| | Turkana Boma | 2 | 21st June 1999 |
| | **Total** | **5** | |
| **Total tree days** | | **16** | |

### 5.2.3 Visitor identification

Ideally all visitors would have been identified to species. However this requires (i) prior knowledge of the visitor fauna and (ii) the ability to accurately identify visitors during observations. Identification of visitors whilst they are foraging on flower heads can be difficult, and the collection of visitors for identification by expert taxonomists is often the only way to confirm species identifications. Since the same set of flower heads was watched throughout a single day, the capture of visitors during observations for subsequent identification would have meant that those individuals were not available to make subsequent visits. In addition, this might have disturbed other visitors currently on flower heads, and deterred other insects from visiting.

To establish a knowledge of the visitor fauna for the acacias at Mpala, insect visitors were caught over 525 hours on 49 days between 2003 and 2005 (see Table 5.3). On these sampling days, visitors to flower heads were caught throughout the day for *S. brevispica*, *V. drepanolobium*, *V. etbaica*, *V. gerrardii*, *S. mellifera*, *V. tortilis* and *V. xanthophloea*. The dates and total number of sampling hours for each acacia species are shown in Table 5.3. Captured specimens were identified by taxonomists, or with the aid of museum specimens. Bees were identified by Connal

Eardley and flies were identified by John Deeming (Calliphoridae, Muscidae, Sarcophagidae, Tachinidae), David Greathead (Bombyliidae), Jason Londt (Asilidae), Adrian Pont (Muscidae), Andrew Whittington (Syrphidae and other fly taxa) and Nigel Wyatt (Tachinidae). Collections at the Natural History Museum in London and the National Museums of Kenya in Nairobi were used to identify wasps, Coleoptera and some Lepidoptera. Butterflies were identified to species using Larsen (1991).

Table 5.3 Dates on which visitors to flower heads of each acacia species were captured and the numbers of hours of catching per acacia species

| Acacia species | Hours catching | Dates of insect catching | |
|---|---|---|---|
| *S. brevispica* | 156 | 13th May 2003<br>23rd May 2003<br>24th May 2003<br>26th May 2003<br>28th May 2003 | 30th May 2003<br>5th June 2003<br>7th June 2003<br>10th June 2003<br>24th Sep 2003 |
| *V. drepanolobium* | 70 | 6th Sep 2003<br>26th Oct 2003<br>30th Oct 2003<br>7th Nov 2003 | 10th Sep 2004<br>13th Sep 2004<br>7th March 2005<br>13th Sep 2005 |
| *V. etbaica* | 80.5 | 11th Aug 2003<br>13th Aug 2003<br>13th March 2004<br>2nd Aug 2004 | 7th Aug 2004<br>5th Jan 2005<br>7th Jan 2005<br>13th Jan 2005 |
| *V. gerrardii* | 28.5 | 3rd June 2003<br>5th June 2003 | 18th Mar 2003<br>29th July 2004 |
| *S. mellifera* | 79 | 6th Nov 2003<br>27th March 2003<br>6th April 2004<br>16th Feb 2005<br>21st Feb 2005 | 11th March 2005<br>16th March 2005<br>18th March 2005<br>22nd March 2005 |
| *V. nilotica* | 111 | 14th June 2003<br>16th June 2003<br>19th June 2003<br>25th June 2004<br>29th June 2004 | 2nd July 2004<br>6th July 2004<br>20th Dec 2004<br>29th Dec 2004<br>21st July 2005 |
| **Totals** | **525 hours** | **49 days** | |

The identified specimens allowed comparison of visitor assemblages at the species level but did not give accurate information regarding the frequency of visits by each species or their patterns of visitation to flower heads. There is an inevitable trade off between the ability to accurately identify species and the quality of information about their visitation patterns.

These specimens were used to identify visitors during the detailed observations. Whilst most observed visitors could be accurately identified to family level, only a proportion could be identified to genus or species.

### 5.2.4 Comparisons of visitor assemblages

Similarities between visitor assemblages were calculated using proportional similarity (PS; Schoener 1970, Kephart 1983, Horvitz and Schemske 1990) to allow comparison with results obtained by Stone et al. (1998). PS was used to compare the visitor assemblages within and between species.

PS was calculated as follows:

(i) the proportions of the total number of flower head visits attributable to each visitor taxon were calculated for two visitor assemblages

(ii) the modulus of the difference in proportions was calculated for each visitor taxon

(iii) PS = 1 - 0.5 (sum of the modulus values over all visitor taxa)

The value of PS ranges from one (maximum similarity) to zero (no overlap between assemblages). PS can only compare two visitor assemblages in a single calculation.

The degree of overlap between visitor assemblages is likely to depend on the resolution to which visitor taxa are classified. All PS values were calculated twice with visitors classified at different taxonomic levels for each calculation. The first calculation was made with bees and flies (the most frequent visitor taxa) resolved to family with the remaining visitors grouped as wasps, beetles and Lepidoptera (butterflies and moths). The analysis was repeated with all visitors assigned to the broader taxonomic groups: bees, wasps, flies, beetles and Lepidoptera. Since ants are considered to be incidental visitors and ineffective pollinators for acacias, they were excluded in the calculations of PS and from all other comparisons between visitor assemblages.

*(a) Intraspecific variation in floral visitor assemblages*

PS was used to examine variation in visitor assemblages for each species. Assemblages were compared:

(i) for trees sampled on the same day (*S. brevispica*, *V. gerrardii* and *V. nilotica*);
(ii) for trees sampled on different days (*S. brevispica*, *V. drepanolobium*, *V. etbaica*, *V. gerrardii* and *V. nilotica)*;
(iii) between sites (*S. brevispica* and *V. nilotica*);
(iv) between years (*S. brevispica*, *V. gerrardii* and *V. nilotica*).

Visitor assemblages were compared across days within sampling sites for *S. brevispica*, *V. etbaica* and *V. nilotica*, but across days at all sites for *V. gerrardii* and *V. drepanolobium* as fewer trees of these species were sampled at individual sites.

*(b) Interspecific variation in floral visitor assemblages*

Visitor assemblages were compared among species using PS separately for each of the 1999 and 2004-5 data sets. The data collected in 2004 and 2005 were grouped so that a larger data set could be used for comparisons. This was considered to be acceptable since data collection spanned approximately 13 months (21st June 2004-14th July 2005). The 1999 data were examined separately since they were collected five years prior to the remainder of the data.

### 5.2.5 Comparisons of daily patterns of visitation to flower heads

*(a) Overall visitation patterns*

I compared overall patterns of visitation within and between acacia species in two ways. I used Kolmogorov-Smirnov two-sample tests to compare the activity distributions of all visitor taxa between trees sampled at the same site on the same day. This non-parametric test has a null hypothesis of identicality between the two distributions. As multiple tests were carried out, the Bonferroni correction was applied. Seventeen tests were conducted which meant that the modified significance level equivalent to $p=0.05$ for rejection for the null hypothesis was 0.0029. Consideration with a less conservative p value ($p=0.05$) did not affect the results. I did not use this test to compare activity at trees sampled on different days or at different sites because variation in climatic conditions between days could have affected visitor behaviour. Instead, activity patterns were compared informally among trees. This was done graphically by scaling the visitation pattern for each tree from zero to one by dividing the visits for each 30 minute observation period by the maximum number of visits for any one observation period for that tree on that day. As elsewhere, visits by ants were excluded.

*Senegalia mellifera* was excluded from these comparisons since only seven visits were recorded on the single day it was sampled. Since large numbers of visitors were captured on flower heads of *S. mellifera* on insect catching days (see Table 5.3) this was considered to be unrepresentative for the species.

*(b) Patterns of visitation by bees and flies*

*Senegalia brevispica*, *V. gerrardii* and *V. hockii* were all visited by large numbers of bees and flies. The activity patterns of these two groups were compared for individual trees using Kolmogorov-Smirnov two-sample tests. Tests were conducted for twenty-two trees which meant that the threshold significance level for the rejection of the null hypothesis with the Bonferroni correction was 0.0023. Consideration with a less conservative p value ($p=0.05$) did not affect the results.

### 5.2.6 Comparisons of daily patterns of visitation and pollen availability

I compared visitation patterns for bees and flies with pollen availability patterns for trees of six acacia species. I only used data for trees for which pollen availability and visitation were quantified on the same day. Pollen availability and patterns of visitation for bees and flies for a single tree were plotted on the same graph with visits or pollen availability scaled between zero and one for *S. brevispica*, *V. drepanolobium*, *V. etbaica*, *V. gerrardii*, *V. hockii* and *V. nilotica*.

## 5.3 Results

### 5.3.1 Do individual acacia species have characteristic floral visitor assemblages?

The floral visitor assemblages of the Mpala acacia species were dominated by bees and flies, with fewer visits from wasps, beetles, butterflies and moths (Tables

5.4, 5.5). In the detailed observations, bees dominated visits to *V. drepanolobium*, *V. etbaica*, *S. mellifera* and *V. nilotica*, whereas *S. brevispica*, *V. gerrardii* and *V. hockii* were visited by large numbers of bees and flies. Although ants were recorded visiting flower heads of all acacia species they are not considered to be effective pollinators of acacias and have been excluded from all results. Details of the identified visitor species caught on acacia flower heads during capture days are given in Appendix 6.

*(a) Bees*

Bees were the dominant visitors to *V. drepanolobium*, *V. etbaica*, *S. mellifera* and *V. nilotica*, and formed a large proportion of visits to *S. brevispica* flower heads (Tables 5.4, 5.5). Bees formed smaller proportions of visits to *V. gerrardii* and *V. hockii* (Tables 5.4, 5.5). The range of bee taxa visiting flower heads was extremely diverse and included Apidae, Colletidae, Halictidae, Megachilidae and Melittidae. *Apis mellifera* (Apidae) were responsible for the majority of observed bee visits to *V. drepanolobium*, but formed a lower proportion of visits to other acacias in the detailed observations (Tables 5.4, 5.5). Other visiting Apidae included the solitary species *Xylocopa somalica*, *Braunsapis ?bouyssoui*, *Macrogalea candida* and *Ceratina* species, and the social species *Plebeina hildebranti*. Few anthophorid bee visitors in the genera *Amegilla*, *Anthophora* and *Tetraloniella* were recorded. All acacias were visited by species of *Megachile*. Bees in this genus formed the majority of megachilid visits in the detailed observations (Tables 5.4, 5.5). Halictid bees included species in the genera *Lasioglossum*, *Patellapis* and *Halictus* (subfamily Halictinae), and the genera *Pseudapis*, *Nomia* and *Lipotriches* (subfamily Nomiinae). Colletid bee visitors belonged to the genera *Colletes* and *Hylaeus*. A single species of melittid bee, *Melitta katherinae*, was found on *V. gerrardii* flower heads and has been described as a new species (Eardley and Kuhlmann 2006).

*(b) Wasps*

Wasps were observed visiting flower heads of all acacias except *S. mellifera* and *V. hockii* during the detailed observations (Tables 5.4, 5.5), although wasps were caught on *S. mellifera* on capture days (Appendix 6). *Senegalia brevispica* and *V. gerrardii* received the largest proportions of wasp visits in both of the detailed observation data sets (Tables 5.4, 5.5). Most wasp visitors were Sphecidae or Eumenidae, with Chrysididae, Pompilidae, Scoliidae, Tiphiidae and Vespidae visiting in smaller numbers.

### *(c) Flies*

Flies were the dominant visitors to flower heads of *S. brevispica*, *V. gerrardii* and *V. hockii*, and formed relatively small proportions of visits to *V. nilotica*, *V. drepanolobium* and *V. etbaica* (between 4.0% and 21.7%; Tables 5.4, 5.5). *Senegalia mellifera* flower heads were not visited by flies in the detailed observations (Table 5.4). Fly visitors included Bombyliidae, Calliphoridae, Muscidae, Sarcophagidae, Syrphidae and Tachinidae. Calliphorids formed the largest proportion of fly visits for most acacia species in the detailed observations (Tables 5.4, 5.5). The most frequently observed calliphorid genera were *Rhyncomya* and *Isomyia*. Syrphids were the most frequently observed fly taxa for *V. nilotica* in the detailed observations, and were relatively common visitors to *S. brevispica* and *V. drepanolobium* (Table 5.4). Common syrphid genera included *Eristalinus* and *Phytomia*. One muscid species found on five acacia species, *Pyrellia acaciae*, has been described as a new species (Pont and Baldock in press).

### *(d) Beetles*

Beetles were observed on flower heads of *S. brevispica*, *V. gerrardii* and *V. nilotica* in the detailed observations, although formed a low proportion of total visits in three species (Tables 5.4, 5.5). Beetles were caught on all acacia species during capture days. Most of these were small beetles in the family Chrysomelidae which often remained on individual flower heads for several hours and seldom moved between flower heads or trees.

### *(e) Lepidoptera*

Lepidopteran visitors were caught on all acacias, although formed a relatively low proportion of visits for most species (Tables 5.4, 5.5). Visitors included butterflies in the families Hesperiidae, Lycaenidae, Nymphalidae and Pieridae and moths in the family Arctiidae (clearwing moths).

Table 5.4 Visitation by different insect taxa to flower heads of acacia species between June 2004 and July 2005 during detailed observations for (a) main visitor groups and (b) the more common families of bee and fly visitors. Data presented in (a) are the percentage of total visitation by all taxa contributed by a particular taxon. Data presented in (b) are the percentage of total visits for either bees or flies contributed by a particular taxon within that group.

(a)

| Acacia species | Bees | Wasps | Diptera | Coleoptera | Lepidoptera | Total visits |
|---|---|---|---|---|---|---|
| *S. brevispica* | 32.2 | 10.4 | 47.1 | 0.7 | 8.9 | 1234 |
| *V. drepanolobium* | 92.5 | 3.1 | 4.0 | 0.0 | 0.2 | 548 |
| *V. etbaica* | 76.6 | 1.1 | 21.7 | 0.0 | 0.6 | 175 |
| *V. gerrardii* | 12.5 | 12.5 | 64.1 | 5.3 | 4.7 | 471 |
| *S. mellifera* | 71.4 | 0.0 | 0.0 | 0.0 | 28.6 | 7 |
| *V. nilotica* | 76.5 | 0.7 | 17.6 | 4.8 | 0.1 | 1809 |

(b)

| Acacia species | *Apis mellifera* | other Apidae | Colletidae | Halictidae | Megachilidae | Calliphoridae | Syrphidae | Bombyliidae | Other Diptera |
|---|---|---|---|---|---|---|---|---|---|
| *S. brevispica* | 13.9 | 2.8 | 23.9 | 9.1 | 40.3 | 33.0 | 20.8 | 0.0 | 46.9 |
| *V. drepanolobium* | 89.7 | 3.2 | 0.0 | 1.4 | 4.1 | 63.6 | 22.7 | 9.1 | 4.5 |
| *V. etbaica* | 9.0 | 61.2 | 0.0 | 1.5 | 24.6 | 47.4 | 0.0 | 0.0 | 52.6 |
| *V. gerrardii* | 0.0 | 0.0 | 1.7 | 21.7 | 43.3 | 62.3 | 4.0 | 9.3 | 24.5 |
| *S. mellifera* | 20.0 | 40.0 | 0.0 | 0.0 | 20.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *V. nilotica* | 0.4 | 3.0 | 0.1 | 2.0 | 87.9 | 38.7 | 51.6 | 2.5 | 7.2 |

Table 5.5 Visitation by different insect taxa to flower heads of acacia species in June 1999 during detailed observations for (a) main visitor groups and (b) the more common families of bee and fly visitors. Data presented in (a) are the percentage of total visitation by all taxa contributed by a particular taxon. Data presented in (b) are the percentage of total visits for either bees or flies contributed by a particular taxon within that group.

(a)

| Acacia species | Bees | Wasps | Diptera | Coleoptera | Lepidoptera | Total visits |
|---|---|---|---|---|---|---|
| *S. brevispica* | 51.1 | 4.4 | 51.1 | 1.4 | 2.3 | 1308 |
| *V. gerrardii* | 24.1 | 9.9 | 54.0 | 1.7 | 10.3 | 6269 |
| *V. hockii* | 17.0 | 0.0 | 83.0 | 0.0 | 0.0 | 165 |
| *V. nilotica* | 74.7 | 0.6 | 15.5 | 9.2 | 0.0 | 490 |

(b)

| Acacia species | *Apis mellifera* | other Apidae | Colletidae | Halictidae | Megachilidae | Calliphoridae | Syrphidae | Bombyliidae | Other Diptera |
|---|---|---|---|---|---|---|---|---|---|
| *S. brevispica* | 0.7 | 0.4 | 0.0 | 98.9 | 0.0 | 91.2 | 8.7 | 0.1 | 0.0 |
| *V. gerrardii* | 19.1 | 0.4 | 0.0 | 67.5 | 9.6 | 88.0 | 7.8 | 0.0 | 4.1 |
| *V. hockii* | 0.0 | 0.0 | 0.0 | 96.4 | 3.6 | 93.4 | 6.6 | 0.0 | 0.0 |
| *V. nilotica* | 2.2 | 1.4 | 0.0 | 73.8 | 22.7 | 100.0 | 0.0 | 0.0 | 0.0 |

### 5.3.2. How variable are the floral visitor assemblages for individual acacia species?

*(a) Comparison of conspecific trees sampled on the same day*

Visitor assemblages for pairs of trees of the same species sampled on the same day at the same site were generally similar in each of *S. brevispica*, *V. gerrardii* and *V. nilotica* (Table 5.6). Assemblages were less similar between pairs of *V. nilotica* trees on 23rd June 2005 and *V. brevispica* trees on 27th June and 7th July 2005 (Table 5.6). Comparisons with similar PS values at both taxonomic resolutions indicate that the specific fly and bee taxa were similar between pairs of trees sampled on the same day.

Table 5.6 Proportional similarities (PS) of floral visitor assemblages for pairs of *S. brevispica*, *V. gerrardii* and *V. nilotica* trees sampled on the same day at the same location. Proportional similarities were calculated with visitors grouped at low and high taxonomic resolutions. A value of 1 indicates maximum similarity and a value of 0 represents no overlap in visitor assemblages.

| Species and date | Site | PS with higher taxonomic resolution | PS with lower taxonomic resolution |
|---|---|---|---|
| *S. brevispica* | | | |
| 9th June 1999 | High Dam | 0.77 | 0.77 |
| 9th June 1999 | High Dam | 0.58 | 0.59 |
| 9th June 1999 | High Dam | 0.78 | 0.79 |
| 13th June 2005 | High Dam | 0.67 | 0.75 |
| 27th June 2005 | High Dam | 0.48 | 0.51 |
| 7th July 2005 | Junction | 0.46 | 0.56 |
| 8th July 2005 | Junction | 0.55 | 0.89 |
| *V. gerrardii* | | | |
| 12th June 1999 | Mongoose | 0.69 | 0.71 |
| 16th June 1999 | High Dam | 0.74 | 0.77 |
| 28th July 2004 | High Dam | 0.69 | 0.84 |
| *V. nilotica* | | | |
| 23rd June 2005 | Turkana Boma | 0.49 | 0.49 |
| 24th June 2005 | Turkana Boma | 0.62 | 0.64 |
| 28th June 2005 | Turkana Boma | 0.95 | 0.97 |
| 29th June 2005 | Turkana Boma | 0.91 | 0.93 |
| 30th June 2005 | Turkana Boma | 0.88 | 0.89 |

### *(b) Comparison of conspecific visitor assemblages between days*

The extent of overlap in visitor assemblages varied across days for all acacias at both taxonomic resolutions. Findings are summarised by species:

#### *(i) S. brevispica*

The mean PS values across days with taxa classed at the higher taxonomic resolution were less than 0.5 for *S. brevispica* at all sites (Table 5.7). The overlap in visitor assemblages at this resolution varied between 0 and 0.76 across all sites, with only two comparisons with PS values greater than 0.6 (Table 5.8). Visitor assemblages were more similar across days when visitors were grouped at the lower taxonomic resolution, with mean PS values between 0.55 and 0.76 at each site (Table 5.8). The visitor assemblages for trees at Junction were least similar among days at the higher resolution (Table 5.8). On most days, visitor taxa were a mixture of bees and flies, with bees forming the greatest proportions of visits on some days and flies on others (Table 5.18). No fly visitors were observed on 18th August and 6th September 2004 at Turkana Boma and no bee visitors were observed on 24th May 2005 at Junction. Fly visitors were a mixture of calliphorids and syrphids, whilst bee visitors included *Apis mellifera*, other apid bees, colletids, halictids and megachilids in varying proportions (Table 5.18). Lepidoptera and wasps contributed considerable numbers of visits to *S. brevispica* flower heads on several days (Table 5.18).

#### *(ii) V. drepanolobium*

Visitor assemblages for *V. drepanolobium* varied least, with high proportions of bee visitors on all three sampling days (Tables 5.7, 5.9, 5.19a). On 10th September and 13th September 2004 *Apis mellifera* was the dominant visitor. On 17th September 2004 approximately half of bee visits were by other apid bees, megachilid and halictid bees, resulting in a lower PS value at the higher taxonomic resolution in comparisons with the other two days (Tables 5.9, 5.19a).

Table 5.7 Mean PS across sampling days (± 1 SE) at each site for *S. brevispica*, *V. etbaica* and *V. nilotica*. *V. drepanolobium* and *V. gerrardii* were sampled on few days at each site therefore mean PS was calculated across days at all sites for these species. Proportional similarities were calculated with visitors grouped at low and high taxonomic resolutions. A value of 1 indicates maximum similarity and a value of 0 represents no overlap in visitor assemblages. Full tables of the PS values between pairs of days are given in Appendix 5.2.

| Species | Sites and year | Mean PS with higher taxonomic resolution | Mean PS with lower taxonomic resolution |
|---|---|---|---|
| *S. brevispica* | Turkana Boma 2004 | 0.28 ± 0.09 | 0.76 ± 0.04 |
| | High Dam 2005 | 0.45 ± 0.04 | 0.67 ± 0.04 |
| | Junction 2005 | 0.46 ± 0.08 | 0.55 ± 0.07 |
| *V. drepanolobium* | Junction and TB 2004 | 0.62 ± 0.14 | 0.96 ± 0.01 |
| *V. etbaica* | Turkana Boma 2004 | 0.33 ± 0.15 | 0.62 ± 0.11 |
| *V. gerrardii* | HD, J and TB 2004 | 0.61 ± 0.05 | 0.69 ± 0.05 |
| | MG, HD and TB | 0.59 ± 0.04 | 0.71 ± 0.04 |
| *V. nilotica* | Turkana Boma 2004 | 0.78 ± 0.07 | 0.92 ± 0.02 |
| | Junction 2004 | 0.28 ± 0.23 | 0.34 ± 0.21 |
| | Turkana Boma 2005 | 0.57 ± 0.03 | 0.71 ± 0.04 |

Table 5.8 Proportional similarities of floral visitor assemblages for *S. brevispica* between days at (a) Turkana Boma in 2004, (b) High Dam in 2005 and (c) Junction in 2005, with visitors grouped at (i) a higher taxonomic resolution and (ii) a lower taxonomic resolution. A value of 1 indicates maximum similarity and a value of 0 represents no overlap in visitor assemblages.

(a) Between days at Turkana Boma in 2004

(i)

| | 18th Aug | 20th Aug | 6th Sep |
|---|---|---|---|
| 21st July | 0.00 | 0.14 | 0.15 |
| 18th Aug | | 0.52 | 0.44 |
| 20th Aug | | | 0.44 |

(ii)

| | 18th Aug | 20th Aug | 6th Sep |
|---|---|---|---|
| 21st July | 0.76 | 0.73 | 0.77 |
| 18th Aug | | 0.68 | 0.96 |
| 20th Aug | | | 0.68 |

(b) Between days at High Dam in 2005

(i)

| | 13th June | 17th June | 27th June |
|---|---|---|---|
| 25th May | 0.50 | 0.43 | 0.33 |
| 13th June | | 0.61 | 0.43 |
| 17th June | | | 0.39 |

(ii)

| | 13th June | 17th June | 27th June |
|---|---|---|---|
| 25th May | 0.61 | 0.64 | 0.67 |
| 13th June | | 0.87 | 0.67 |
| 17th June | | | 0.57 |

(c) Between days at Junction in 2005

(i)

| | 24th June | 7th July | 8th July |
|---|---|---|---|
| 20th May | 0.55 | 0.21 | 0.43 |
| 24th June | | 0.37 | 0.76 |
| 7th July | | | 0.41 |

(ii)

| | 24th June | 7th July | 8th July |
|---|---|---|---|
| 20th May | 0.55 | 0.56 | 0.51 |
| 24th June | | 0.39 | 0.88 |
| 7th July | | | 0.42 |

Table 5.9 Proportional similarities of floral visitor assemblages for *V. drepanolobium* between days with visitors grouped at (i) a higher taxonomic resolution (ii) a lower taxonomic resolution. A value of 1 indicates maximum similarity and a value of 0 represents no overlap in visitor assemblages. TB: Turkana Boma, J: Junction

(i)

| | 13th Sep TB | 17th Sep J |
|---|---|---|
| 10th Sep J | 0.91 | 0.48 |
| 13th Sep TB | | 0.48 |

(ii)

| | 13th Sep TB | 17th Sep J |
|---|---|---|
| 10th Sep J | 0.96 | 0.95 |
| 13th Sep TB | | 0.97 |

*(iii) V. etbaica*

The three *V. etbaica* trees sampled at Turkana Boma in 2004 had little similarity among visitor assemblages in comparisons at the higher taxonomic resolution, with the trees sampled on 13th September and 27th August having almost completely different visitor taxa (Tables 5.10, 5.19b). Similarities were greater at the lower taxonomic resolution (Table 5.10). Bees formed the majority of visits on 21st and 27th August whilst on 13th September similar proportions of bees and flies were found (Table 5.19b). The proportions of specific bee and fly taxa varied across days (Table 5.19b). Bee visitors were a mixture of *Apis mellifera*, other apid bees (mostly *Plebeina hildebranti*), halictids and megachilids, and flies were either calliphorids, muscids or sarcophagids (Table 5.19b).

Table 5.10 Proportional similarities of floral visitor assemblages for *V. etbaica* between days at Turkana Boma with visitors grouped at (i) a higher taxonomic resolution and (ii) a lower taxonomic resolution. A value of 1 indicates maximum similarity and a value of 0 represents no overlap in visitor assemblages.

(i)

| | 27th Aug | 13th Sep |
|---|---|---|
| 21st Aug | 0.42 | 0.52 |
| 27th Aug | | 0.04 |

(ii)

| | 27th Aug | 13th Sep |
|---|---|---|
| 21st Aug | 0.82 | 0.61 |
| 27th Aug | | 0.43 |

*(iv) V. gerrardii*

The mean PS values for *V. gerrardii* were relatively high with visitor assemblages grouped at both taxonomic resolutions (Table 5.7). The degree of overlap in visitor assemblages between days varied considerably, although all PS values calculated at the low taxonomic resolution were greater than 0.55 and all but two were greater than 0.5 at the higher taxonomic resolution (Tables 5.11, 5.12). Flies, most of which were calliphorids, formed the largest proportions of visits on all days (Table 5.20). Bees visited flower heads on all but two sampling days, with *Apis mellifera*, halictid and megachilid bees the main taxa in varying proportions (Table 5.20). Large proportions of wasp visitors were recorded on two days (Table 5.20).

Table 5.11 Proportional similarities of floral visitor assemblages for *V. gerrardii* (a) between days in 2004, (b) between days in 1999 and (c) between years, with visitors grouped at (i) a higher taxonomic resolution and (ii) a lower taxonomic resolution. A value of 1 indicates maximum similarity and a value of 0 represents no overlap in visitor assemblages. TB: Turkana Boma, J: Junction, MG: Mongoose, HD: High Dam

(a) Between days in 2004

(i)

| | 30th July Junction | 18th Aug TB |
|---|---|---|
| 28th July HD | 0.63 | 0.52 |
| 30th July J | | 0.68 |

(ii)

| | 30th July Junction | 18th Aug TB |
|---|---|---|
| 28th July HD | 0.69 | 0.61 |
| 30th July J | | 0.77 |

(b) Between days in 1999

(i)

| | 12th June MG | 16th June HD | 17th June HD | 21st June TB |
|---|---|---|---|---|
| 6th June MG | 0.63 | 0.45 | 0.34 | 0.54 |
| 12th June MG | | 0.68 | 0.51 | 0.75 |
| 16th June HD | | | 0.58 | 0.68 |
| 17th June HD | | | | 0.74 |

(ii)

| | 12th June MG | 16th June HD | 17th June HD | 21st June TB |
|---|---|---|---|---|
| 6th June MG | 0.74 | 0.57 | 0.55 | 0.63 |
| 12th June MG | | 0.84 | 0.61 | 0.75 |
| 16th June HD | | | 0.74 | 0.83 |
| 17th June HD | | | | 0.85 |

*(v) V. nilotica*

Mean PS values were high at both taxonomic resolutions for *V. nilotica* sampled at Turkana Boma in 2004 (Table 5.7). Visitors on these days were mainly megachilid bees, with smaller proportions of calliphorid flies and halictid bees (Table 5.21b). At Junction a single *V. nilotica* tree was sampled on three days (30th July, 10th September and 17th September 2004). The visitor assemblages were more similar to each other on the days in September than to that on the 30th July (Table 5.12b, 5.21c). Whilst bee visitors dominated in September, the visitors were mainly flies on 30th July (Table 5.21c).

PS values for *V. nilotica* calculated among eight days at Turkana Boma in 2005 were extremely variable ranging from 0.17 to 0.98 (high resolution) and 0.36 to 0.99 (low resolution) (Table 5.12c). Visitor assemblages differed most when compared between the 23rd or 24th June and other sampling days (Table 5.12c). On these days flies formed greater proportions of visits than bees (Table 5.21d) whilst on all other days bees formed the largest proportion of visits (Table 5.21d). Most bee visitors were megachilids, with other apid bees visiting on 12th and 13th July (Table 5.21d).

Table 5.12 Proportional similarities of floral visitor assemblages for *V. nilotica* between days at (a) Turkana Boma in 2004, (b) at Junction in 2004 and (c) at Turkana Boma in 2004, with visitors grouped at (i) a higher taxonomic resolution and (ii) a lower taxonomic resolution. A value of 1 indicates maximum similarity and a value of 0 represents no overlap in visitor assemblages.

(a) Between days at Turkana Boma in 2004

(i)

| | 22nd June | 16th July |
|---|---|---|
| 21st June | 0.70 | 0.72 |
| 22nd June | | 0.91 |

(ii)

| | 22nd June | 16th July |
|---|---|---|
| 21st June | 0.91 | 0.89 |
| 22nd June | | 0.95 |

(b) Between days at Junction in 2004

(i)

| | 10th Sep | 17th Sep |
|---|---|---|
| 30th June | 0.06 | 0.04 |
| 10th Sep | | 0.75 |

(ii)

| | 10th Sep | 17th Sep |
|---|---|---|
| 30th June | 0.03 | 0.24 |
| 10th Sep | | 0.75 |

(c) Between days at Turkana Boma in 2005

(i)

| | 23rd June | 24th June | 28th June | 29th June | 30th June | 12th July | 13th July | 14th July |
|---|---|---|---|---|---|---|---|---|
| 21st June | 0.32 | 0.55 | 0.68 | 0.67 | 0.70 | 0.76 | 0.68 | 0.68 |
| 23rd June | | 0.71 | 0.17 | 0.16 | 0.19 | 0.36 | 0.25 | 0.39 |
| 24th June | | | 0.43 | 0.41 | 0.47 | 0.57 | 0.49 | 0.55 |
| 28th June | | | | 0.98 | 0.93 | 0.54 | 0.58 | 0.90 |
| 29th June | | | | | 0.92 | 0.54 | 0.59 | 0.57 |
| 30th June | | | | | | 0.56 | 0.57 | 0.56 |
| 12th July | | | | | | | 0.75 | 0.69 |
| 13th July | | | | | | | | 0.66 |

(ii)

| | 23rd June | 24th June | 28th June | 29th June | 30th June | 12th July | 13th July | 14th July |
|---|---|---|---|---|---|---|---|---|
| 21st June | 0.40 | 0.56 | 0.84 | 0.83 | 0.86 | 0.87 | 0.84 | 0.76 |
| 23rd June | | 0.81 | 0.36 | 0.35 | 0.39 | 0.53 | 0.37 | 0.29 |
| 24th June | | | 0.53 | 0.53 | 0.58 | 0.69 | 0.54 | 0.46 |
| 28th June | | | | 0.99 | 0.93 | 0.77 | 0.98 | 0.93 |
| 29th June | | | | | 0.93 | 0.76 | 0.97 | 0.93 |
| 30th June | | | | | | 0.80 | 0.95 | 0.86 |
| 12th July | | | | | | | 0.78 | 0.70 |
| 13th July | | | | | | | | 0.92 |

### *(c) Comparison of conspecific visitor assemblages between sites*

### *(i) S. brevispica*

Flies and bees were the most frequent visitors to flower heads of *S. brevispica* at all sites (Table 5.18). Calliphorid flies were the most common fly taxa at all sites, whilst bees were a mixture of apids, colletids, halictids and megachilids in varying proportions (Table 5.18). Visitor assemblages were most similar between Junction and High Dam in 2005 at both taxonomic resolutions (Table 5.13). The trees at these sites were all sampled during June and July 2005. The PS values were much lower in comparisons between Turkana Boma in 2004 (July-Sep) and Junction and High Dam in 2005, although seasonal variation and variation between years might have contributed to differences between sites (Table 5.13). The visitor assemblages at High Dam in 1999 were most similar to the 2005 data at both Junction and High Dam at the lower taxonomic resolution (Table 5.13). PS values at the higher taxonomic resolution were much lower, probably due to the large number of halictid bees observed in 1999 (Table 5.18).

Table 5.13 Proportional similarities of floral visitor assemblages for *S. brevispica* between sites with visitors grouped at (i) a higher taxonomic resolution and (ii) a lower taxonomic resolution. A value of 1 indicates maximum similarity and a value of 0 represents no overlap in visitor assemblages. TB: Turkana Boma, HD: High Dam and J: Junction

(i)

| | TB 2004 | HD 2005 | J 2005 |
|---|---|---|---|
| HD 1999 | 0.25 | 0.26 | 0.34 |
| TB 2004 | | 0.43 | 0.36 |
| HD 2005 | | | 0.63 |

(ii)

| | TB 2004 | HD 2005 | J 2005 |
|---|---|---|---|
| HD 1999 | 0.58 | 0.83 | 0.86 |
| TB 2004 | | 0.43 | 0.49 |
| HD 2005 | | | 0.86 |

### *(ii) V. nilotica*

Bees were the main visitors to *V. nilotica* in all years at Turkana Boma. At Junction, the proportions of flies and bees were approximately equal (Table 5.14). When the visitor assemblages at Junction were compared with those at Turkana Boma in all three years, the PS values were relatively high at the lower taxonomic resolution (Table 5.21a). The PS values were lower when visitor assemblages were compared at the higher taxonomic resolution (Table 5.14). Bee visitors at Turkana Boma were mainly megachilids in 2004 and 2005, and halictids in 1999 (Table

5.21a). Bee visitors at Junction in 2004 were mainly megachilids with small proportions of apid bees (Table 5.21a).

Table 5.14 Proportional similarities of floral visitor assemblages for *V. nilotica* between sites with visitors grouped at (i) a higher taxonomic resolution and (ii) a lower taxonomic resolution. A value of 1 indicates maximum similarity and a value of 0 represents no overlap in visitor assemblages. TB: Turkana Boma, J: Junction

(i)

| | Junction 2004 | TB 2005 | TB 1999 |
|---|---|---|---|
| TB 2004 | 0.45 | 0.85 | 0.32 |
| J 2004 | | 0.50 | 0.21 |
| TB 2005 | | | 0.27 |

(ii)

| | Junction 2004 | TB 2005 | TB 1999 |
|---|---|---|---|
| TB 2004 | 0.60 | 0.93 | 0.91 |
| J 2004 | | 0.66 | 0.65 |
| TB 2005 | | | 0.96 |

### *(d) Comparison of conspecific visitor assemblages between years*

Similarities in visitor assemblages for *S. brevispica* were greatest between 2004 and 2005 at the high taxonomic resolution, although assemblages were most similar between 1999 and 2005 at the lower taxonomic resolution (Table 5.15, 5.18a). Visitor assemblages were similar across years for *V. gerrardii*, with relatively high PS values at both taxonomic resolutions (Tables 5.16, 5.20a).

Whilst the specific bee taxa visiting *V. nilotica*, mostly megachilid bees, were similar between years in 2004 and 2005, resulting in high PS values (Tables 5.17, 21a), there was greater variation between 1999 and 2004-2005 in terms of specific bee taxa (Tables 5.17, 5.21a). Whereas megachilid bees dominated bee visits in 2004 and 2005, the main bee visitors in 1999 were halictids (Table 5.21a).

Table 5.15 Proportional similarities of floral visitor assemblages for *S. brevispica* between years, with visitors grouped at (i) a higher taxonomic resolution and (ii) a lower taxonomic resolution. A value of 1 indicates maximum similarity and a value of 0 represents no overlap in visitor assemblages.

(i)

| | 2004 | 2005 |
|---|---|---|
| 1999 | 0.25 | 0.31 |
| 2004 | | 0.42 |

(ii)

| | 2004 | 2005 |
|---|---|---|
| 1999 | 0.58 | 0.85 |
| 2004 | | 0.48 |

Table 5.16 Proportional similarities of floral visitor assemblages for *V. gerrardii* between years, with visitors grouped at (i) a higher taxonomic resolution and (ii) a lower taxonomic resolution. A value of 1 indicates maximum similarity and a value of 0 represents no overlap in visitor assemblages.

(i)

| | 1999 |
|---|---|
| 2004 | 0.67 |

(ii)

| | 1999 |
|---|---|
| 2004 | 0.83 |

Table 5.17 Proportional similarities of floral visitor assemblages for *V. nilotica* between years, with visitors grouped at (i) a higher taxonomic resolution and (ii) a lower taxonomic resolution. A value of 1 indicates maximum similarity and a value of 0 represents no overlap in visitor assemblages.

(i)

| | 2004 | 2005 |
|---|---|---|
| 1999 | 0.29 | 0.27 |
| 2004 | | 0.80 |

(ii)

| | 2004 | 2005 |
|---|---|---|
| 1999 | 0.92 | 0.96 |
| 2004 | | 0.93 |

### 5.3.3 Do acacia species share floral visitors and do their visits represent a significant proportion of all visits?

*(a) Shared visitor species*

Of the visitor species caught on flower heads, 24 bee, 22 wasp, 26 fly, 12 beetle, six butterfly and one moth species were found on more than one acacia (Appendix 6). Four bee species, *Apis mellifera*, *Braunsapis ?bouyssoui*, *Macrogalea candida* and *Pseudapis* (*Pseudapis*) sp. 1, were caught on all six acacias. Three bees, *Plebeina hildebranti*, *Megachile* (*Chalicodoma*) sp. 1, *Megachile* (*Chalicodoma*) sp. 2, two wasps, *Cerceris* sp. 1 and *Cerceris* sp. 2, four flies, *Rhyncomya forcipata*, *Musca lusoria*, *Eristalinus taeniops* and *Phytomia incisa*, and one butterfly, *Azanus jesous*, were caught on five acacias (Appendix 6).

Although visitor species were found on multiple acacias, the capture data gives no information regarding the frequency of visits, or the similarity of visitor assemblages between species. These have to be compared at lower taxonomic resolutions using the detailed observation data.

Table 5.18 Variation in insect taxa visiting flower heads of *S. brevispica*. Data are percentage of total visitation by all taxa contributed by a particular taxon. Data presented are the variation (a) between sites and years (HD: High Dam, TB: Turkana Boma, J: Junction), (b) between days at Turkana Boma in 2004, (c) between days at High Dam in 2005 and (d) between days at Junction in 2005.

(a)

| | Total bees | *Apis mellifera* | other Apidae | Colletidae | Halictidae | Megachilidae | Total Diptera | Calliphoridae | Syrphidae | Bombyliidae | wasp | Coleoptera | Lepidoptera | Total flower visits |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| HD 1999 | 41.7 | 0.3 | 0.2 | 0.0 | 41.3 | 0.0 | 51.1 | 46.6 | 4.4 | 0.1 | 4.4 | 0.4 | 2.3 | 1308 |
| TB 2004 | 78.8 | 24.8 | 4.4 | 12.4 | 16.8 | 8.0 | 10.2 | 1.5 | 0.0 | 0.0 | 8.8 | 0.7 | 1.5 | 137 |
| HD 2005 | 24.9 | 3.8 | 0.7 | 10.0 | 1.1 | 6.2 | 51.9 | 13.4 | 9.6 | 0.0 | 6.2 | 0.2 | 16.5 | 551 |
| J 2005 | 27.8 | 0.0 | 0.2 | 4.2 | 1.3 | 21.1 | 51.5 | 21.2 | 12.5 | 0.0 | 17.8 | 15.0 | 3.1 | 546 |

(b)

| | Total bees | *Apis mellifera* | other Apidae | Colletidae | Halictidae | Megachilidae | Total Diptera | Calliphoridae | Syrphidae | Bombyliidae | wasp | Coleoptera | Lepidoptera | Total flower visits |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 21st July | 75.7 | 0.0 | 0.0 | 23.0 | 31.1 | 8.1 | 5.4 | 1.4 | 0.0 | 0.0 | 16.2 | 1.4 | 1.4 | 74 |
| 18th Aug | 100.0 | 100.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 7 |
| 20th Aug | 67.7 | 51.6 | 0.0 | 2.6 | 3.1 | 16.1 | 32.3 | 3.2 | 4.0 | 0.0 | 5.7 | 0.0 | 3.5 | 31 |
| 6th Sep | 96.0 | 44.0 | 24.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 4.0 | 25 |

(c)

| | Total bees | *Apis mellifera* | other Apidae | Colletidae | Halictidae | Megachilidae | Total Diptera | Calliphoridae | Syrphidae | Bombyliidae | wasp | Coleoptera | Lepidoptera | Total flower visits |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 25th May | 48.6 | 28.6 | 0.0 | 2.9 | 0.0 | 17.1 | 40.0 | 8.6 | 11.4 | 0.0 | 0.0 | 2.9 | 2.9 | 35 |
| 13th June | 17.7 | 0.0 | 1.4 | 5.4 | 2.0 | 8.8 | 58.5 | 11.2 | 6.8 | 0.0 | 6.5 | 0.0 | 17.3 | 294 |
| 17th June | 21.4 | 0.0 | 0.0 | 19.4 | 0.0 | 1.9 | 68.0 | 35.9 | 6.8 | 0.0 | 1.0 | 0.0 | 9.7 | 103 |
| 27th June | 38.7 | 9.2 | 0.0 | 15.1 | 0.0 | 0.0 | 25.2 | 0.8 | 18.5 | 0.0 | 11.8 | 0.0 | 24.4 | 119 |

(d)

| | Total bees | *Apis mellifera* | other Apidae | Colletidae | Halictidae | Megachilidae | Total Diptera | Calliphoridae | Syrphidae | Bombyliidae | wasp | Coleoptera | Lepidoptera | Total flower visits |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 20th May | 13.2 | 0.0 | 0.7 | 11.2 | 0.0 | 1.3 | 40.1 | 0.7 | 9.9 | 0.0 | 39.5 | 2.6 | 2.6 | 152 |
| 24th May | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 85.4 | 24.4 | 24.4 | 0.0 | 14.6 | 0.0 | 0.0 | 41 |
| 7th July | 56.4 | 0.0 | 0.0 | 2.6 | 3.1 | 49.3 | 33.0 | 26.4 | 4.0 | 0.0 | 5.7 | 0.0 | 3.5 | 227 |
| 8th July | 3.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.8 | 87.3 | 35.7 | 27.0 | 0.0 | 2.4 | 2.4 | 4.0 | 126 |

Table 5.19 Variation in insect taxa visiting flower heads of (a) *V. drepanolobium* across days at Turkana Boma (TB) and Junction in 2004 and (b) *V. etbaica* across days at Turkana Boma in 2004. Data are percentage of total visitation by all taxa contributed by a particular taxon.

(a)

| | Total bees | *Apis mellifera* | other Apidae | Colletidae | Halictidae | Megachilidae | Total Diptera | Calliphoridae | Syrphidae | Bombyliidae | wasp | Coleoptera | Lepidoptera | Total flower visits |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 10th Sep Junction | 95.5 | 93.8 | 0.0 | 0.0 | 1.8 | 0.0 | 3.6 | 1.8 | 1.8 | 0.0 | 0.9 | 0.0 | 0.0 | 112 |
| 13th Sep TB | 91.9 | 88.1 | 0.0 | 0.0 | 0.0 | 1.7 | 4.2 | 3.3 | 0.0 | 0.6 | 3.9 | 0.0 | 0.0 | 360 |
| 17th Sep Junction | 90.8 | 43.4 | 21.1 | 0.0 | 6.6 | 19.7 | 3.9 | 0.0 | 3.9 | 0.0 | 2.6 | 0.0 | 1.3 | 76 |

(b)

| | Total bees | *Apis mellifera* | other Apidae | Colletidae | Halictidae | Megachilidae | Total Diptera | Calliphoridae | Syrphidae | Bombyliidae | wasp | Coleoptera | Lepidoptera | Total flower visits |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 21st Aug | 80.5 | 2.4 | 36.6 | 0.0 | 4.9 | 36.6 | 19.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 41 |
| 27th Aug | 98.7 | 12.7 | 84.8 | 0.0 | 0.0 | 1.3 | 1.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 79 |
| 13th Sep | 41.8 | 1.8 | 0.0 | 0.0 | 0.0 | 30.9 | 52.7 | 32.7 | 0.0 | 0.0 | 3.6 | 0.0 | 1.8 | 55 |

Table 5.20 Variation in insect taxa visiting flower heads of *V. gerrardii*. Data are percentage of total visitation by all taxa contributed by a particular taxon. Data presented are the variation (a) between years, (b) between days and sites in 1999 and (c) between days and sites in 2004 (TB: Turkana Boma).

(a)

| | Total bees | *Apis mellifera* | other Apidae | Colletidae | Halictidae | Megachilidae | Total Diptera | Calliphoridae | Syrphidae | Bombyliidae | wasp | Coleoptera | Lepidoptera | Total flower visits |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1999 | 24.1 | 4.6 | 0.1 | 0.0 | 16.3 | 2.3 | 54.0 | 47.5 | 4.2 | 0.0 | 9.9 | 1.7 | 10.3 | 6269 |
| 2004 | 12.7 | 0.0 | 0.0 | 0.2 | 2.8 | 5.5 | 64.1 | 39.9 | 2.5 | 5.9 | 12.5 | 5.3 | 4.7 | 471 |

(b)

| | Total bees | *Apis mellifera* | other Apidae | Colletidae | Halictidae | Megachilidae | Total Diptera | Calliphoridae | Syrphidae | Bombyliidae | wasp | Coleoptera | Lepidoptera | Total flower visits |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 6th June Mongoose | 13.5 | 0.0 | 0.0 | 0.0 | 13.5 | 0.0 | 42.9 | 29.6 | 6.2 | 0.0 | 21.3 | 3.6 | 18.7 | 1951 |
| 12th June Mongoose | 34.0 | 6.6 | 0.0 | 0.0 | 22.4 | 5.0 | 48.9 | 46.0 | 2.9 | 0.0 | 6.6 | 1.1 | 9.4 | 2697 |
| 16th June High Dam | 36.2 | 23.1 | 0.9 | 0.0 | 10.3 | 1.7 | 62.9 | 52.3 | 9.6 | 0.0 | 0.7 | 0.2 | 0.0 | 458 |
| 17th June High Dam | 10.2 | 0.5 | 0.3 | 0.0 | 2.1 | 0.2 | 87.7 | 0.0 | 0.3 | 0.0 | 0.9 | 0.5 | 0.5 | 666 |
| 21st June TB | 19.2 | 0.0 | 0.0 | 0.0 | 19.2 | 0.0 | 73.9 | 0.0 | 4.1 | 0.0 | 3.2 | 0.0 | 3.7 | 437 |

(c)

| | Total bees | *Apis mellifera* | other Apidae | Colletidae | Halictidae | Megachilidae | Total Diptera | Calliphoridae | Syrphidae | Bombyliidae | wasp | Coleoptera | Lepidoptera | Total flower visits |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 28th July High Dam | 15.1 | 0.0 | 0.0 | 0.3 | 3.3 | 6.5 | 55.6 | 38.0 | 3.0 | 6.5 | 14.1 | 3.3 | 5.5 | 397 |
| 30th July Junction | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 76.9 | 46.2 | 0.0 | 3.1 | 4.6 | 18.5 | 0.0 | 65 |
| 18th Aug TB | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 100.0 | 77.8 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 9 |

Table 5.21 Variation in insect taxa visiting flower heads of *V. nilotica*. Data are percentage of total visitation by all taxa contributed by a particular taxon. Data presented are the variation (a) between sites and years (TB: Turkana Boma, J: Junction), (b) between days at Turkana Boma in 2004 and (c) between days at Junction in 2004.

(a)

| | Total bees | *Apis mellifera* | other Apidae | Colletidae | Halictidae | Megachilidae | Total Diptera | Calliphoridae | Syrphidae | Bombyliidae | wasp | Coleoptera | Lepidoptera | Total flower visits |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| TB 1999 | 74.7 | 1.6 | 1.0 | 0.0 | 55.1 | 16.9 | 15.5 | 15.5 | 0.0 | 0.0 | 0.6 | 9.2 | 0.0 | 490 |
| TB 2004 | 83.8 | 1.4 | 0.0 | 0.0 | 8.5 | 73.2 | 10.6 | 8.8 | 0.0 | 0.0 | 0.0 | 5.6 | 0.0 | 284 |
| TB 2005 | 77.9 | 0.1 | 1.6 | 0.1 | 0.2 | 69.4 | 16.2 | 3.4 | 11.7 | 0.0 | 0.9 | 4.9 | 0.1 | 1391 |
| J 2004 | 47.0 | 0.0 | 14.2 | 0.0 | 0.0 | 32.1 | 46.3 | 38.1 | 0.7 | 6.0 | 0.0 | 2.2 | 0.0 | 137 |

(b)

| | Total bees | *Apis mellifera* | other Apidae | Colletidae | Halictidae | Megachilidae | Total Diptera | Calliphoridae | Syrphidae | Bombyliidae | wasp | Coleoptera | Lepidoptera | Total flower visits |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 21st June | 79.2 | 3.2 | 0.0 | 0.0 | 16.8 | 59.2 | 9.6 | 8.8 | 0.0 | 0.0 | 0.0 | 11.2 | 0.0 | 125 |
| 22nd June | 88.5 | 0.0 | 0.0 | 0.0 | 1.0 | 85.6 | 9.6 | 6.7 | 0.0 | 0.0 | 0.0 | 1.9 | 0.0 | 104 |
| 16th July | 85.5 | 0.0 | 0.0 | 0.0 | 3.6 | 81.8 | 14.5 | 12.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 57 |

(c)

| | Total bees | *Apis mellifera* | other Apidae | Colletidae | Halictidae | Megachilidae | Total Diptera | Calliphoridae | Syrphidae | Bombyliidae | wasp | Coleoptera | Lepidoptera | Total flower visits |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 30th July | 3.4 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 88.5 | 88.5 | 87.9 | 1.7 | 0.0 | 3.4 | 0.0 | 58 |
| 10th Sep | 92.9 | 0.0 | 32.1 | 0.0 | 0.0 | 60.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 28 |
| 17th Sep | 75.0 | 0.0 | 20.8 | 0.0 | 0.0 | 54.2 | 16.7 | 0.0 | 0.0 | 16.7 | 0.0 | 2.1 | 0.0 | 48 |

Table 5.21 (cont.) Variation in insect taxa visiting flower heads of *V. nilotica*. Data are percentage of total visitation by all taxa contributed by a particular taxon. Data presented are the variation (a) between sites and years (TB: Turkana Boma, J: Junction), (b) between days at Junction in 2004 and (c) between days at Turkana Boma in 2005.

(d)

| | Total bees | *Apis mellifera* | other Apidae | Colletidae | Halictidae | Megachilidae | Total Diptera | Calliphoridae | Syrphidae | Bombyliidae | wasp | Coleoptera | Lepidoptera | Total flower visits |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 21st June | 76.4 | 3.6 | 0.0 | 0.0 | 0.0 | 60.0 | 5.5 | 0.0 | 5.5 | 0.0 | 0.0 | 18.2 | 0.0 | 55 |
| 23rd June | 29.0 | 0.0 | 0.0 | 0.0 | 0.0 | 8.5 | 65.9 | 18.2 | 46.0 | 0.0 | 0.0 | 5.1 | 0.0 | 176 |
| 24th June | 45.8 | 0.0 | 0.0 | 0.8 | 0.0 | 34.4 | 47.3 | 8.4 | 38.9 | 0.0 | 2.3 | 4.6 | 0.0 | 131 |
| 28th June | 92.6 | 0.0 | 0.0 | 0.0 | 0.0 | 91.8 | 3.0 | 0.4 | 2.6 | 0.0 | 0.0 | 4.3 | 0.0 | 231 |
| 29th June | 93.1 | 0.0 | 0.0 | 0.0 | 0.0 | 91.6 | 2.5 | 0.0 | 0.0 | 0.0 | 0.5 | 3.9 | 0.0 | 407 |
| 30th June | 86.5 | 0.0 | 0.0 | 0.0 | 0.0 | 86.1 | 6.4 | 1.2 | 5.2 | 0.0 | 3.2 | 4.0 | 0.0 | 251 |
| 12th July | 69.8 | 0.0 | 9.3 | 0.0 | 0.0 | 46.5 | 18.6 | 0.0 | 7.0 | 0.0 | 0.0 | 11.6 | 0.0 | 43 |
| 13th July | 91.9 | 0.0 | 24.3 | 0.0 | 4.1 | 52.7 | 5.4 | 0.0 | 1.4 | 0.0 | 0.0 | 2.7 | 0.0 | 74 |
| 14th July | 95.7 | 0.0 | 0.0 | 0.0 | 0.0 | 44.8 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 3.4 | 23 |

*(b) Similarity of visitor assemblages among acacia species*

Overall, there were greater similarities among species' visitor assemblages in the 1999 data set than the 2004-5 data set. This could be due in part to the timescales over which data were collected. The 1999 data were collected over a period of three weeks whereas the 2004-5 data set comprised trees sampled between June 2004 and July 2005. There is therefore a greater likelihood that similar visitor taxa were present throughout the 1999 data set, than for the 2004-5 data.

When bees and flies were classed to family level, *S. brevispica* and *V. gerrardii* had the most similar visitor assemblages in both data sets (Tables 5.22, 5.23). These species had similar proportions of visits from calliphorid flies and megachilid bees in the 2004-5 data set and similar proportions of visits from halictid bees, calliphorid flies and syrphid flies in the 1999 data set (Tables 5.4, 5.5). No other pairs of species had visitor assemblages with a PS of greater than 0.5 at the higher taxonomic resolution in 2004-5. In the 1999 data set, *V. hockii* had similar visitor assemblages to both *S. brevispica* and *V. gerrardii* (Table 5.23). All three species had similar proportions of visits from halictid bees, calliphorid flies and syrphid flies (Table 5.5). The assemblages of *S. brevispica* and *V. nilotica* were relatively similar in 1999, with a PS of 0.58 (Table 5.23).

When all visitors were classed at the lower taxonomic resolution there were greater similarities among more pairs of species in the 2004-5 data set (Table 5.22). Four species had very similar visitor assemblages at this resolution: *V. etbaica*, *V. drepanolobium*, *S. mellifera* and *V. nilotica* (Table 5.22). All of these species had high proportions of bee visits (Table 5.4).

For most species pairs in the 1999 data set there was little difference between the PS values calculated using the different taxonomic groupings (Table 5.23).

Table 5.22 Proportional similarities of floral visitor assemblages between all species sampled in 2004 and 2005 with visitors grouped at (i) a higher taxonomic resolution (ii) a lower taxonomic resolution. A value of 1 indicates maximum similarity and a value of 0 represents no overlap in visitor assemblages. Values greater than 0.5 are in bold.

(i)

| | *V. drepanolobium* | *V. etbaica* | *V. gerrardii* | *S. mellifera* | *V. nilotica* |
|---|---|---|---|---|---|
| *S. brevispica* | 0.16 | 0.30 | **0.60** | 0.28 | 0.36 |
| *V. drepanolobium* | | 0.18 | 0.14 | 0.22 | 0.14 |
| *V. etbaica* | | | 0.30 | 0.40 | 0.17 |
| *V. gerrardii* | | | | 0.14 | 0.28 |
| *S. mellifera* | | | | | 0.22 |
| *V. nilotica* | | | | | |

(ii)

| | *V. drepanolobium* | *V. etbaica* | *V. gerrardii* | *S. mellifera* | *V. nilotica* |
|---|---|---|---|---|---|
| *S. brevispica* | 0.40 | **0.56** | **0.76** | 0.41 | **0.51** |
| *V. drepanolobium* | | **0.82** | 0.20 | **0.72** | **0.82** |
| *V. etbaica* | | | 0.36 | **0.72** | **0.95** |
| *V. gerrardii* | | | | 0.17 | 0.36 |
| *S. mellifera* | | | | | **0.71** |
| *V. nilotica* | | | | | |

Table 5.23 Proportional similarities of floral visitor assemblages between all species sampled in June 1999 with visitors grouped at (i) a higher taxonomic resolution (ii) a lower taxonomic resolution. A value of 1 indicates maximum similarity and a value of 0 represents no overlap in visitor assemblages. Values greater than 0.5 are in bold.

(i)

| | *V. gerrardii* | *V. hockii* | *V. nilotica* |
|---|---|---|---|
| *S. brevispica* | **0.75** | **0.67** | **0.58** |
| *V. gerrardii* | | **0.69** | 0.38 |
| *V. hockii* | | | 0.33 |
| *V. nilotica* | | | |

(ii)

| | *V. gerrardii* | *V. hockii* | *V. nilotica* |
|---|---|---|---|
| *S. brevispica* | **0.82** | **0.68** | **0.58** |
| *V. gerrardii* | | **0.71** | 0.42 |
| *V. hockii* | | | 0.32 |
| *V. nilotica* | | | |

### 5.3.4 Do daily patterns of visitation vary within and between acacia species?

*(a) Overall visitation patterns*

All acacia trees had fewer visits at the start and end of the sampling day, and a visitation peak between approximately 9.00 and 16.00 (Table 5.24, Figs. 5.1-5.2, 5.4-5.6, 5.8-5.9). Some trees had a single clear overall visitation peak, whilst others had several peaks of visitor activity. Few visits were observed on any species before 8.00, although one *V. nilotica* tree sampled at Turkana Boma on 7th June 1999 had a large number of visits in the first observation period, between 6.40 and 7.10 (Fig. 5.8a). All but one of these 27 visits were from calliphorid flies, and bees did not visit until later in the day.

Visitation patterns varied across trees in all species (Fig. 5.1). Peak visitation for *V. gerrardii* and *V. nilotica* varied between 10.00 and 15.30-16.00 (Fig. 5.1, Table 5.24). Peak visitation for *S. brevispica* varied between 12.00 and 16.00 and for *V. drepanolobium* between 9.00 and 12.30. Visitation patterns varied least for *V. etbaica*, with visitation peaks occurring between 11.30 and 14.00 in all trees.

Daily temporal patterns of visitation to flower heads were not noticeably different between species (Figs. 5.2, 5.4-5.6, 5.8-5.9). Visitation peaks for all except *V. hockii* occurred within a similar time window, although there was least overlap between *S. brevispica* and *V. drepanolobium* (Fig. 5.1). Species with more samples had the greatest variation in peak visitation times among trees and the increased variation could be because more trees were sampled (Table 5.24).

*(b) Variation in visitation patterns among visitor taxa*

Bees were the main visitors to *V. drepanolobium*, *V. etbaica* and *V. nilotica* (Tables 5.4, 5.5). *Senegalia brevispica*, *V. gerrardii* and *V. hockii* all received large proportions of visits from flies and bees (Tables 5.4, 5.5). Flies were often active before bees and tended to visit flower heads over a longer time period, arriving earlier in the morning (Figs. 5.3, 5.5, 5.7), and on some days remaining on flower heads after bees had finished visiting (Figs. 5.3e, f, 5.7c, d). In all three species, the maximum visitation rate for flies usually occurred earlier in the day than for bees (Figs. 5.3, 5.5, 5.7).

Bee and fly visitation patterns were not significantly different in individual *V. hockii* or *S. brevispica* trees. Bee and fly visitation patterns were significantly different for one *V. gerrardii* tree on 17th June 1999 at High Dam (Kolmogorov-Smirnov two-sample test: Z=2.000, N=8, $p<0.001$), however there were no significant differences between fly and bee visitation patterns in other *V. gerrardii* trees.

Table 5.24 The range of times over which peak visitation occurred for all visitors, bees and flies, for all trees of each acacia species. Flies formed fewer than 5% of visits for *V. drepanolobium.*

| | Number of trees sampled | Time of peak visitation | Time of peak bee visitation | Time of peak fly visitation |
|---|---|---|---|---|
| *S. brevispica* | 19 | 12.00-16.00 | 10.00-16.30 | 8.00-16.30 |
| *V. drepanolobium* | 3 | 9.00-12.30 | 9.00-12.30 | - |
| *V. etbaica* | 3 | 11.30-14.00 | 11.30-14.00 | 11.30-14.00 |
| *V. gerrardii* | 11 | 10.00-16.00 | 10.00-15.00 | 10.00-16.00 |
| *V. hockii* | 1 | 8.30-9.00 | 12.30-13.00 | 8.30-9.00 |
| *V. nilotica* | 25 | (7.00) 10.00-15.30 | 10.00-15.30 | 6.40-15.30 |

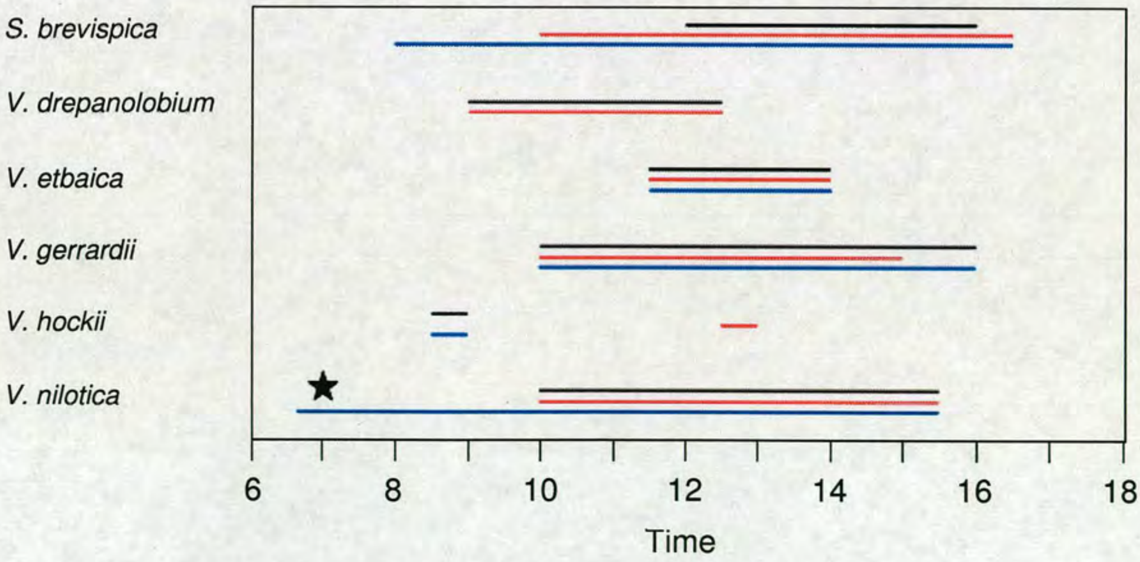


Figure 5.1 The range of times over which peak visitation occurred for all visitors (black), bees (red) and flies (blue) for all trees of each acacia species. The star indicates that peak visitation for a single *V. nilotica* tree occurred at a very different time in comparison to all other trees of the same species.

*(ii) Variation between trees sampled on the same day*

Conspecific trees sampled on the same day generally had similar patterns of visitation in *S. brevispica*, *V. gerrardii* and *V. nilotica* (Figs. 5.2, 5.6, 5.8a, 5.9). Some trees sampled on the same day had different visitation patterns. For example, the peak visitation rates for two *S. brevispica* trees sampled on 7th July 2005 occurred at approximately 12.00 and 15.30 (Fig. 5.2b) and the peak visitation rates for two trees sampled at High Dam on 13th June 2005 occurred at approximately 12.00 and 14.00 (Fig. 5.2c). Peak visitation for flies and bees occurred at similar times to the overall peak in all four trees therefore differences between trees were not due to differing visitation patterns between the two visitor groups (e.g. 5.3b, e). There were no significant differences between the visitation patterns of conspecific trees sampled at the same site on the same day for *S. brevispica*, *V. gerrardii* or *V. nilotica.*

*(c) Variation for individual trees between days*

Most trees sampled on multiple days showed similar visitation patterns across days, although for some trees peak visitation occurred at slightly different times on different days (Table 5.25, Figs. 5.2b, 5.4a, 5.6a, 5.8c, 5.9).

Table 5.25 Individual trees sampled for visitors on multiple days and the approximate times at which peak visitation rates occurred

| Species | Site | Tree number | Dates sampled | Approximate time of peak visitation |
|---|---|---|---|---|
| *S. brevispica* | Junction | tree 1 | 7th and 8th July 2005 | 13.00, 15.30 |
| | | tree 2 | 7th and 8th July 2005 | 12.00, 13.00 |
| *V. drepanolobium* | Junction | tree 1 | 10th and 17th Sep 2004 | 12.00 for both |
| *V. gerrardii* | Mongoose | tree 1 | 6th and 12th June 1999 | 10.00, 15.00* |
| *V. nilotica* | Junction | tree 1 | 30th July 2004<br>10th and 17th Sep 2004 | 11.30, 13.00, 14.00 |
| | Turkana Boma | tree 1 | 21st June, 30th June & 14th July 2005 | 12.00, 10.00, 12.00 |
| | Turkana Boma | tree 2 | 23rd June, 24th June, 28th June, 29th June & 30th June 2005 | 10.00, 13.00, 13.00, 13.00, 10.00 |
| | Turkana Boma | tree 3 | 23rd June, 24th June, 28th June, 29th June, 12th July & 13th July 2005 | 13.00, 15.30, 13.00, 13.00, 13.30, 11.00 |

* On 6th June 1999 sampling did not continue past 14.00, however visitation patterns on both days were similar until approximately 13.00 (Fig. 5.8a)

### *(d) Variation between sites and years*

For most species there are not enough samples to meaningfully compare visitation patterns between years or sites. Climatic variation will also affect patterns of visitation between days and across seasons. The species with the greatest number of samples at a single site was *V. nilotica* at Turkana Boma. There was no evidence of significant variation in visitation patterns between trees sampled in 1999, 2004 and 2005 (Figs. 5.8, 5.9). Visitation patterns for *S. brevispica* and *V. gerrardii* were not noticeably different across years (Figs. 5.2, 5.6).

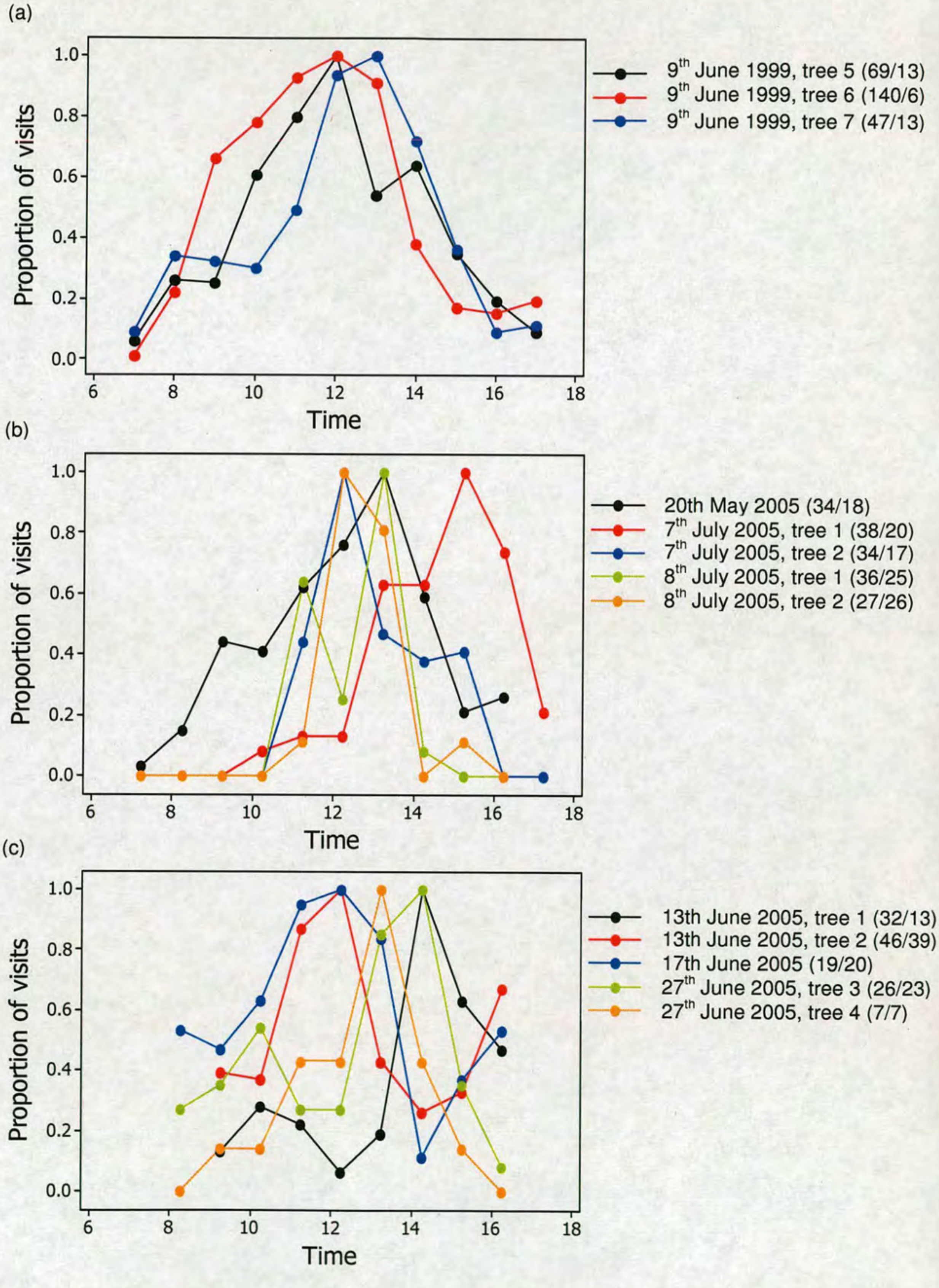


Fig. 5.2 Patterns of visitation to flower heads of *S. brevispica* (a) on 9th June 1999 at High Dam, (b) in 2005 at Junction and (c) in 2005 at High Dam. Data shown are the proportion of the maximum number of visits. The figures in brackets indicate the maximum number of visits per tree followed by the number of flowers observed. Trees are numbered to distinguish between multiple trees of the same species sampled at the same location, or to indicate trees that have been sampled on multiple days.

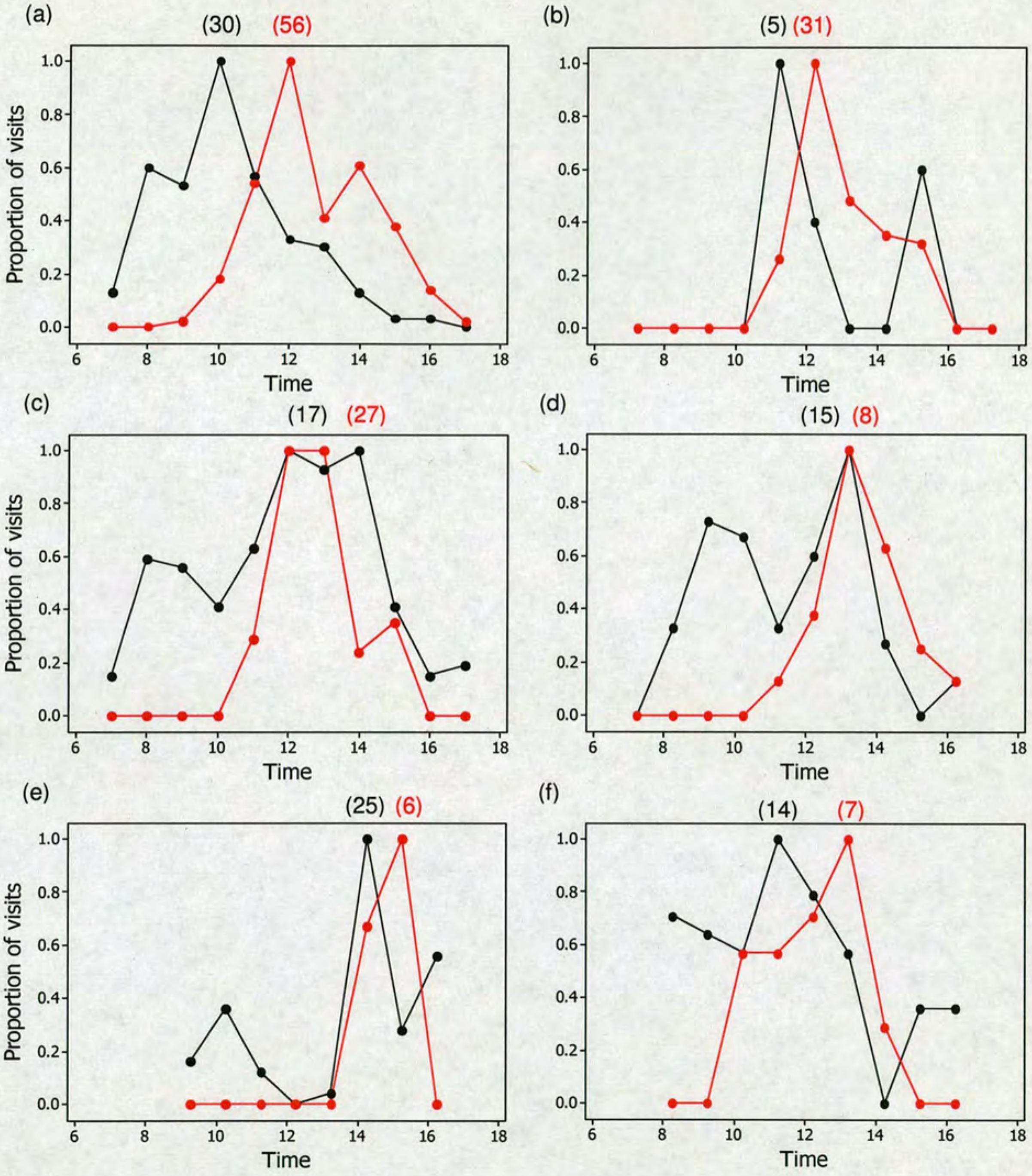
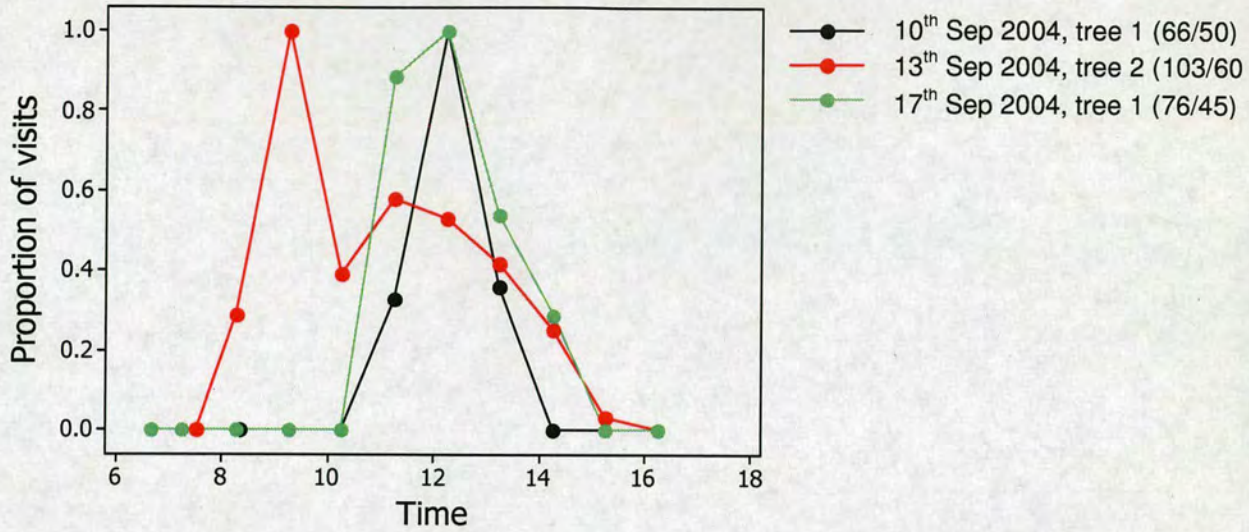


Fig. 5.3 Patterns of visitation to flower heads of *S. brevispica* by flies (blue line) and bees (red line) (a) for tree 1 on 9th June 1999 at High Dam, (b) for tree 2 on 7th July 2005 (c) for tree 3 on 9th June in 2005 at High Dam, (d) on 20th May 2005 at Junction, (e) for tree 1 on 13th June 2005 at High Dam and (f) on 17th June 2005 at High Dam. Data shown are the proportion of the maximum number of visits for that taxon. The figures above peaks show the maximum number of visits for each taxon.

(a)



(b)

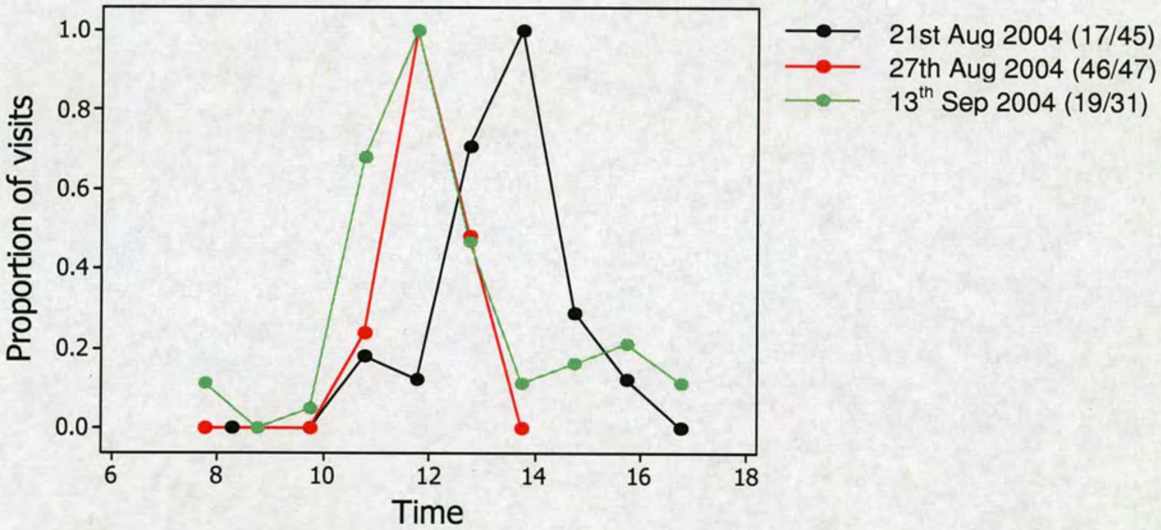


Fig. 5.4 Patterns of visitation to flower heads of (a) *V. drepanolobium* at Turkana Boma and Junction sites and (b) *V. etbaica* at Turkana Boma in 2004. Data shown are the proportion of the maximum number of visits. The figures in brackets indicate the maximum number of visits per tree followed by the number of flowers observed. Trees are numbered to distinguish between multiple trees of the same species sampled at the same location, or to indicate trees that have been sampled on multiple days.

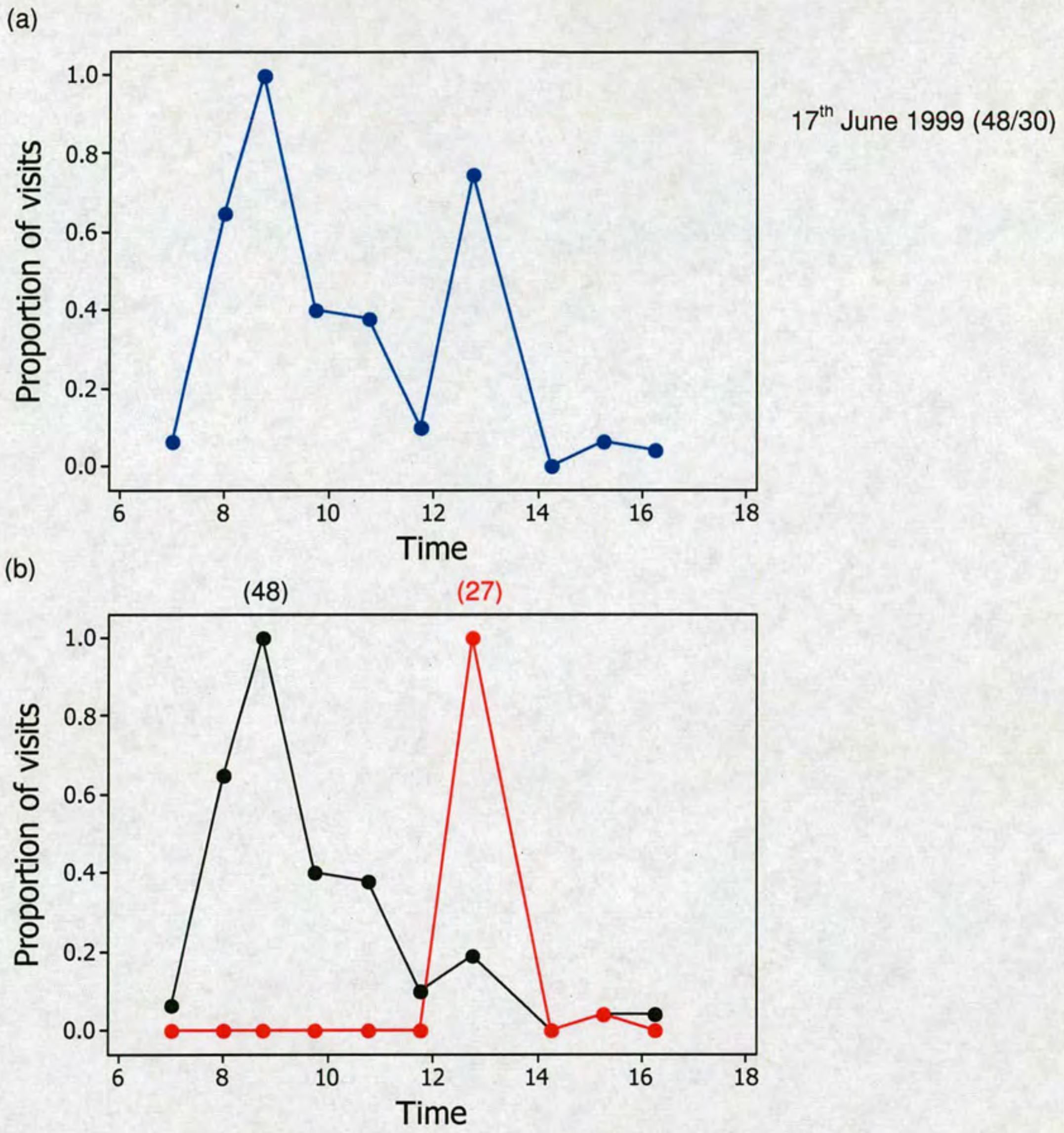


Fig. 5.5 (a) Patterns of visitation to flower heads of *V. hockii* at on 17th June 1999 at High Dam. Data shown are the proportion of the maximum number of visits. The figures in brackets indicate the maximum number of visits per tree followed by the number of flowers observed.

(b) Patterns of visitation to flower heads of *V. hockii* by flies (blue line) and bees (red line) on 17th June 1999 at High Dam. Data shown are the proportion of the maximum number of visits for that taxon. The figures above peaks show the maximum number of visits for each taxon.

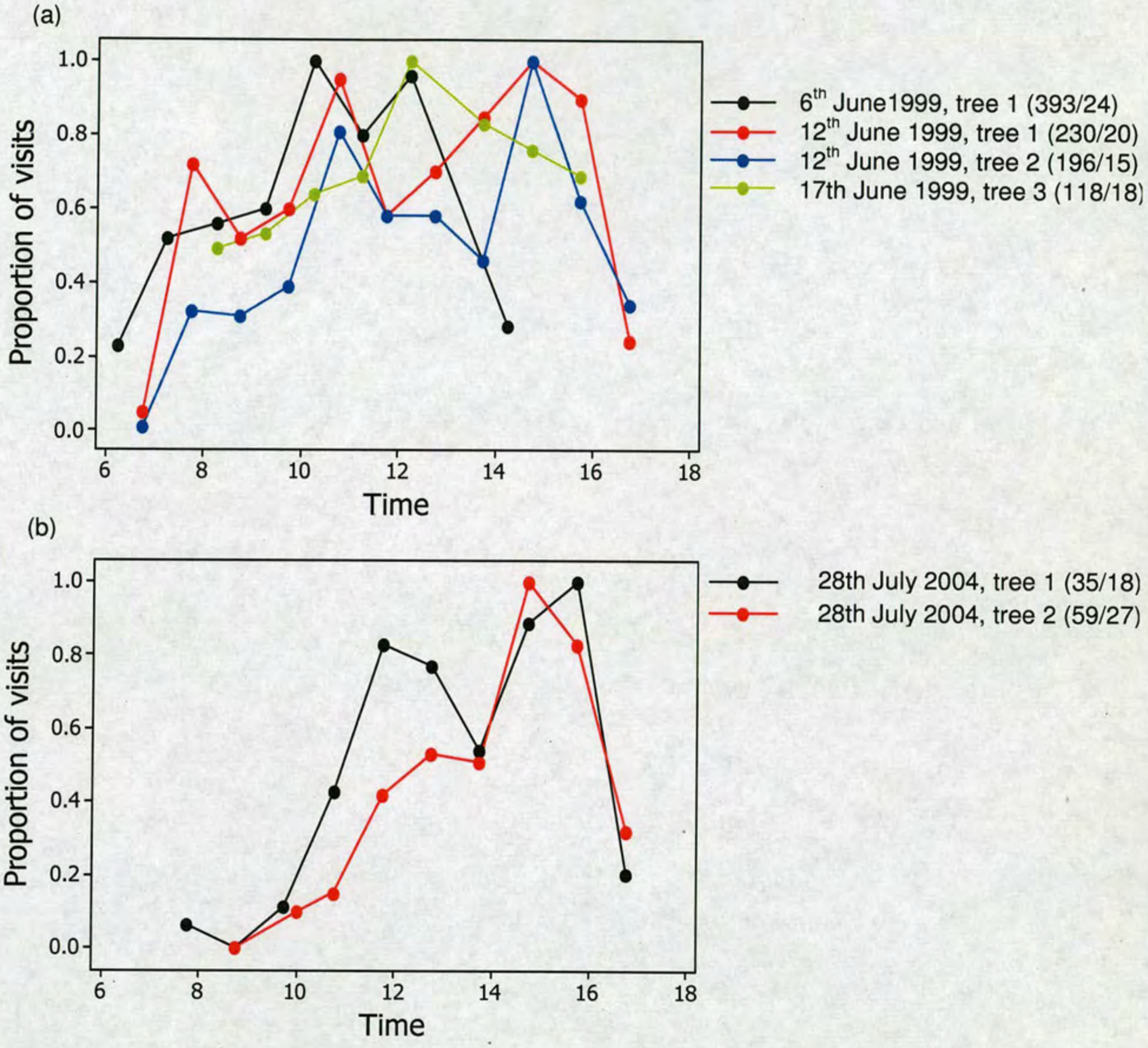


Fig. 5.6 Patterns of visitation to flower heads of *V. gerrardii* (a) in June 1999 at Mongoose (6th and 12th June) and High Dam (16th and 17th June), and (b) on 28th July 2004 at Junction. Data shown are the proportion of the maximum number of visits. The figures in brackets indicate the maximum number of visits per tree followed by the number of flowers observed. Trees are numbered to distinguish between multiple trees of the same species sampled at the same location, or to indicate trees that have been sampled on multiple days.

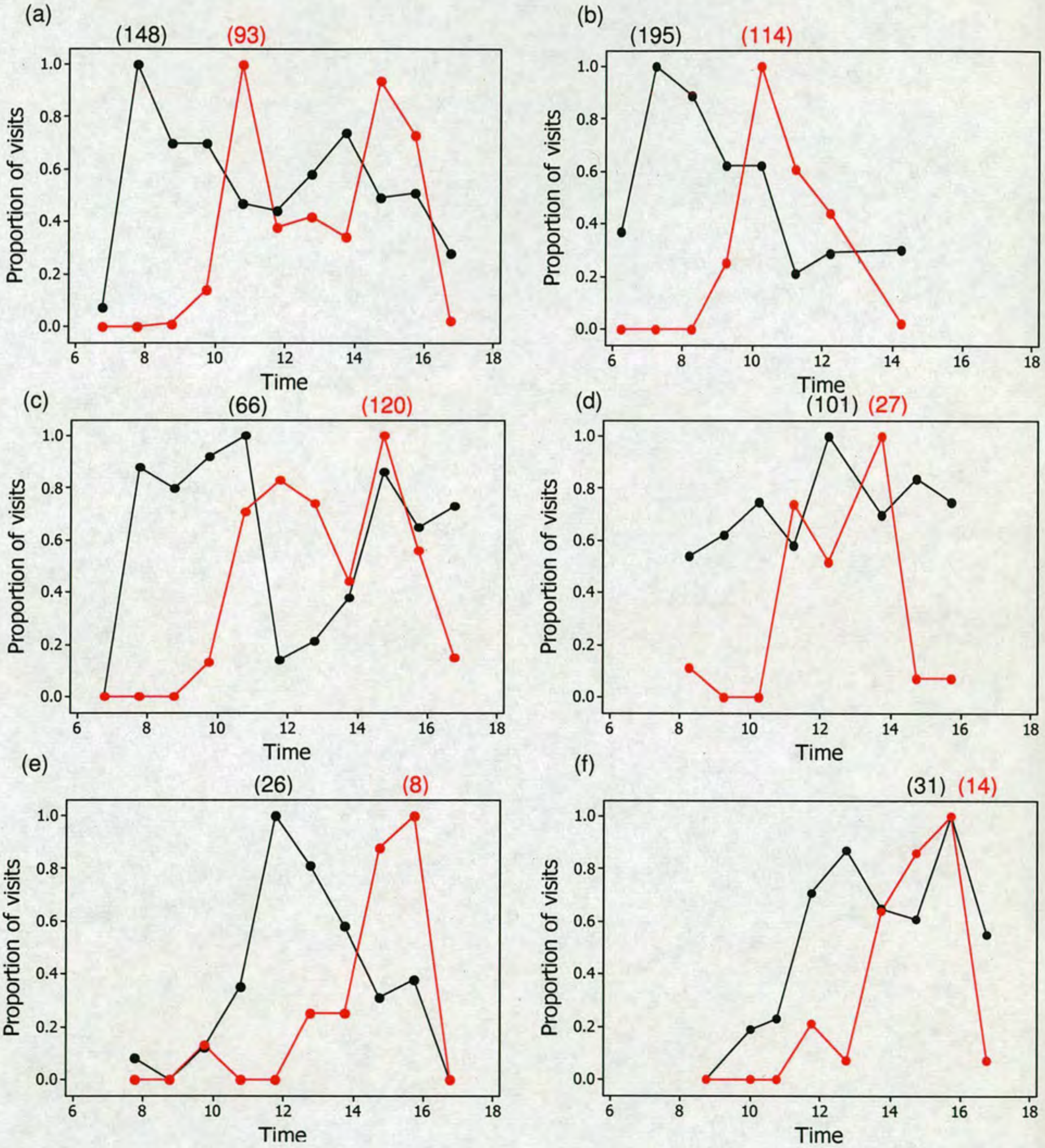


Fig. 5.7 Patterns of visitation to flower heads of *V. gerrardii* by flies (black line) and bees (red line) (a) for tree 1 on 12th June 1999 at Mongoose, (b) on 6th June 1999 at Mongoose (c) for tree 2 on 12th June 1999 at Mongoose, (d) on 17th June 1999 at Junction, (e) for tree 1 on 28th July 2004 at High Dam and (f) for tree 2 on 28th July 2004 at High Dam. Data shown are the proportion of the maximum number of visits for that taxa. The figures above peaks show the maximum number of visits for each taxa.

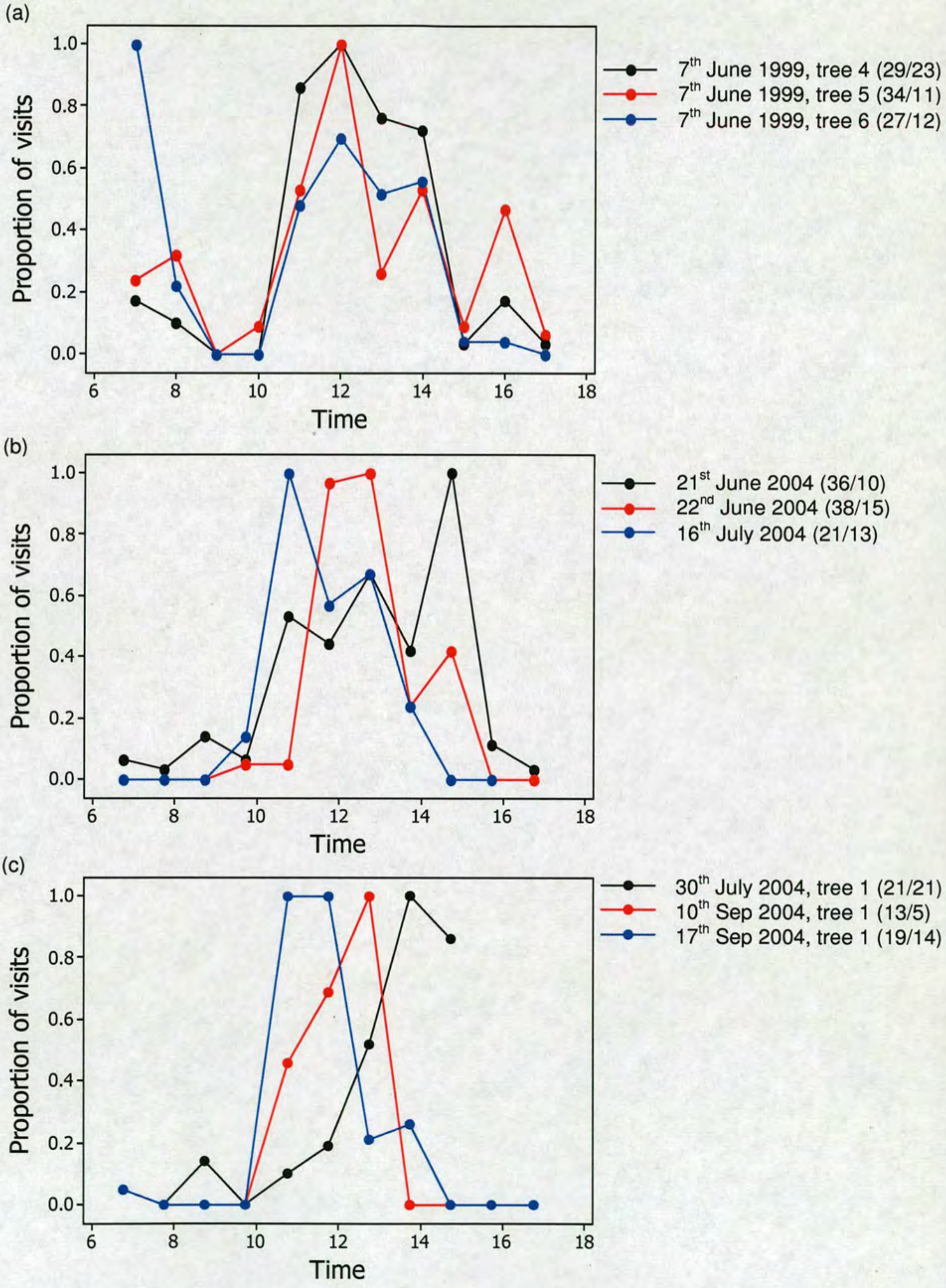


Fig. 5.8 Patterns of visitation to flower heads of *V. nilotica* (a) on 7th June 1999 at Turkana Boma, (b) in 2004 at Turkana Boma and (b) in 2004 at Junction. Data shown are the proportion of the maximum number of visits. The figures in brackets indicate the maximum number of visits per tree followed by the number of flowers observed. Trees are numbered to distinguish between multiple trees of the same species sampled at the same location, or to indicate trees that have been sampled on multiple days.

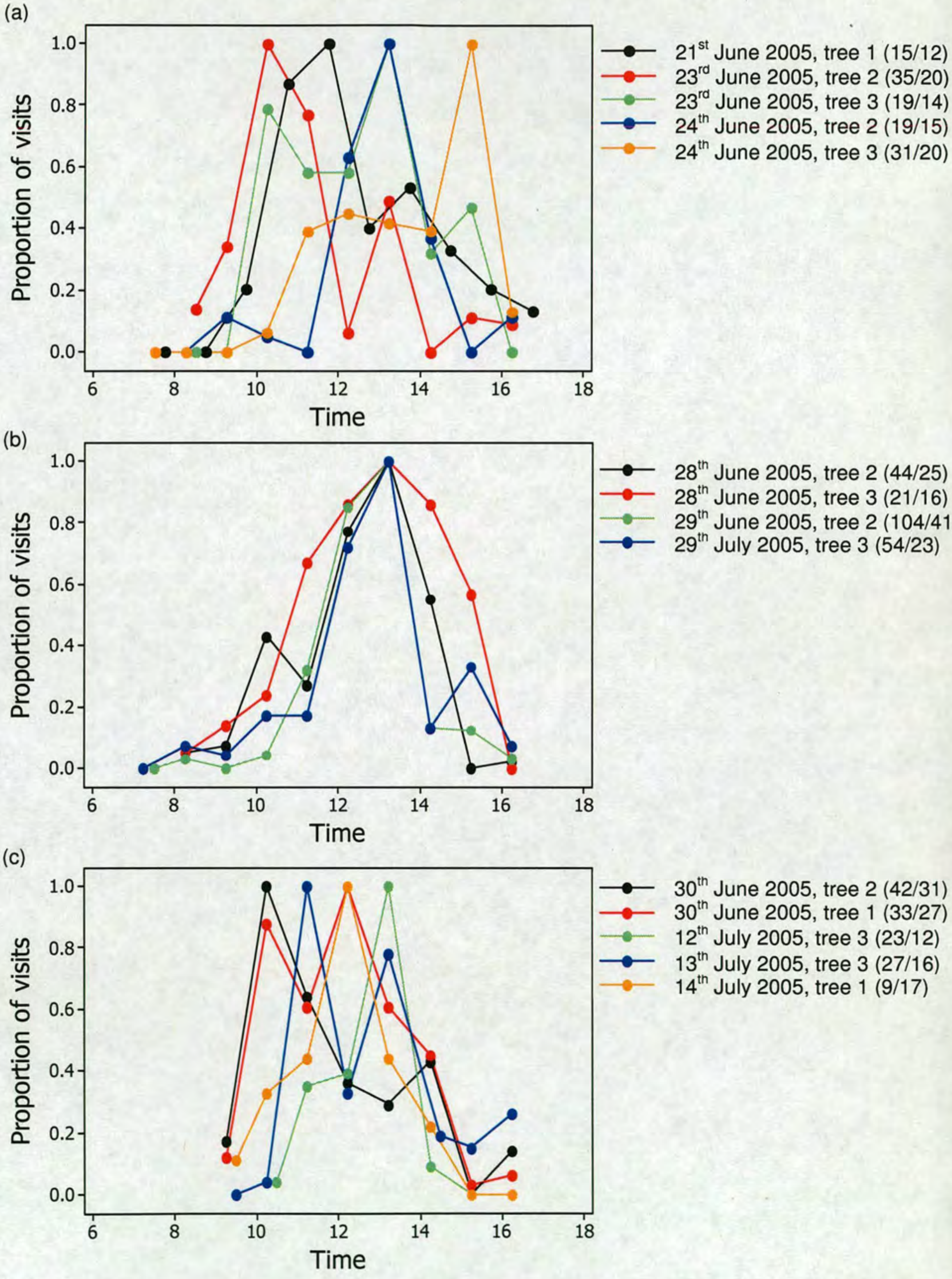


Fig. 5.9 Patterns of visitation to flower heads of *V. nilotica* at Turkana Boma in 2005. Data shown are the proportion of the maximum number of visits. The figures in brackets indicate the maximum number of visits per tree followed by the number of flowers observed. Trees are numbered to distinguish between multiple trees of the same species sampled at the same location, or to indicate trees that have been sampled on multiple days.

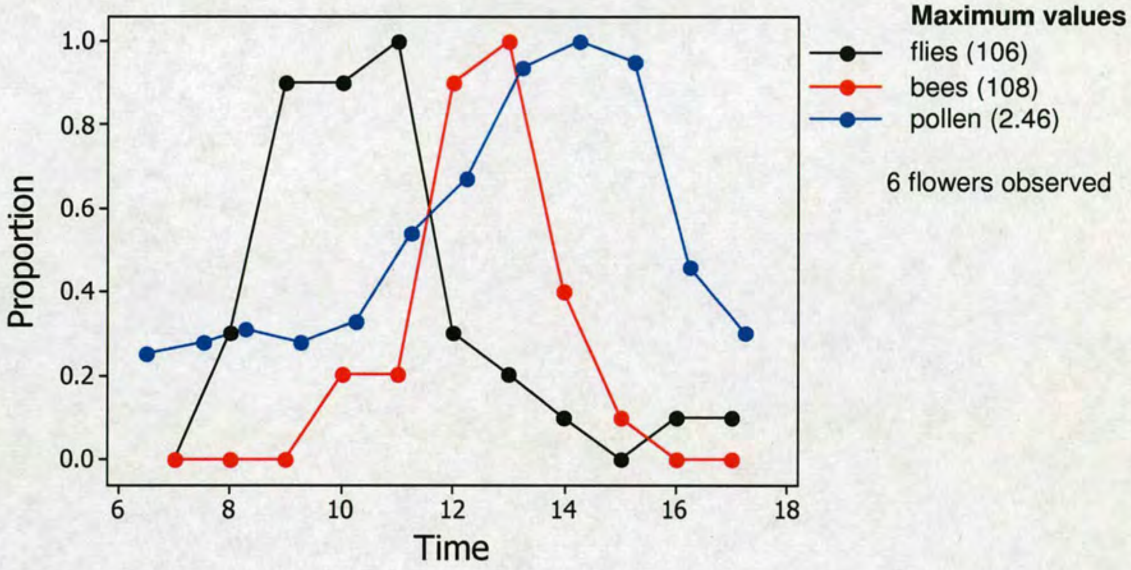
### 5.3.5 Do patterns of visitation track patterns of pollen availability in each acacia species?

Peak bee visitation occurred at a similar time to or after maximum pollen availability in all acacia species except *S. brevispica* (Figs. 5.10-5.16). Maximum pollen availability for the two *S. brevispica* trees occurred after peak bee visitation, however bee visits increased as pollen availability increased and bees could have been harvesting pollen as it was released (Fig. 5.10). The bee visitation peak for *V. drepanolobium* corresponded extremely closely with the pollen availability peak for the tree sampled on 17th September 2005 (Fig. 5.11). The pattern of pollen availability for the same tree on 10th September 2004 was more variable, however peak bee visitation coincided with relatively high levels of pollen availability (Fig. 5.11a). The pollen availability peaks for both *V. etbaica* trees sampled occurred early in the day, and there was a four hour delay before bee visitation peaked on both days (Fig. 5.12a, b).

Peak fly visitation occurred prior to peak pollen availability in *S. brevispica*, *V. hockii* and two *V. gerrardii* trees (Figs. 5.10, Fig. 5.12c, 5.13a, b). In *V. etbaica*, *V. nilotica* and the other four *V. gerrardii* trees peak fly visitation corresponded more closely with peak pollen availability (Figs. 5.12, 5.13c, 5.14, 5.15, 5.16). Patterns of fly visitation matched pollen availability more closely than did bees for two *V. gerrardii* trees sampled on 28th July 2004 (Fig. 5.14) and for *V. etbaica* on 21st August (Fig. 5.12a). However, there were only eight fly visits in total for *V. etbaica* on this day.

The pollen availability patterns for the three *V. nilotica* trees sampled at Turkana Boma in 2004 were erratic, with no single clear peak of pollen availability (Fig. 5.15). Visitor patterns were more consistent, with most bee visits occurring between 11.00 and 15.00 (Fig. 5.15). On 21st June and 16th July bee visits corresponded to relatively high levels of pollen availability, however this was not the case on 22nd June, as pollen availability peaked much later in the day (Fig. 5.15c). However, the pollen to anther ratio just before the bee visitation peak on this day was almost equivalent to that for peaks on other sampling days (Fig. 5.15). There were fewer fly visits for *V. nilotica* than for other species, but visits occurred at similar times to bees (Fig. 5.15).

Bee and fly visitation peaks corresponded to pollen availability peaks on all three days for the *V. nilotica* tree at Junction, although the pollen availability pattern was erratic on 17th September 2004 (Fig. 5.16).


(a) *S. brevispica*, tree 6, 9th June 1999, High Dam

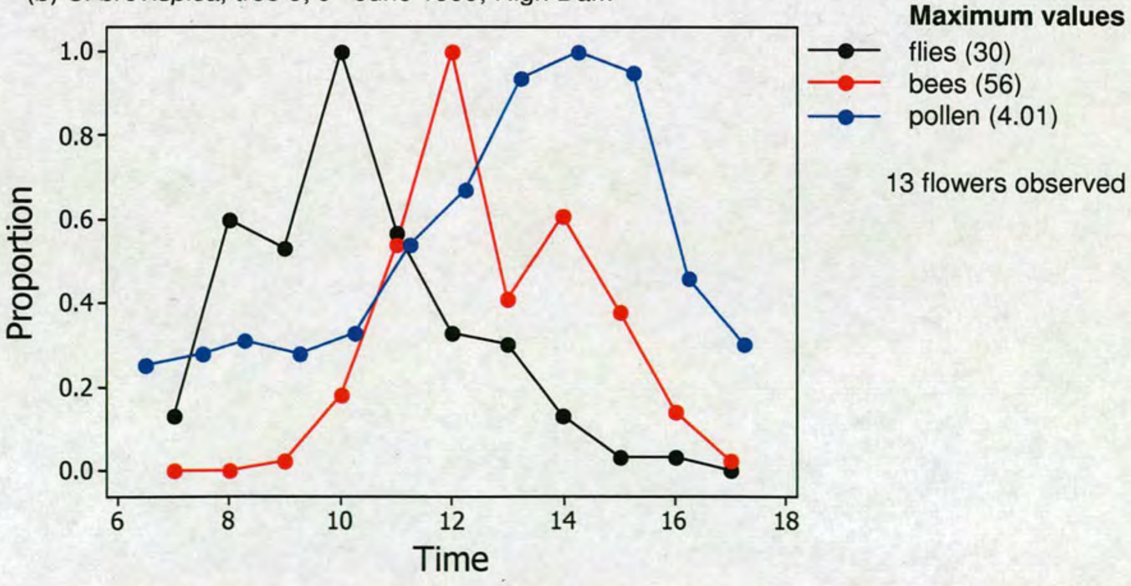
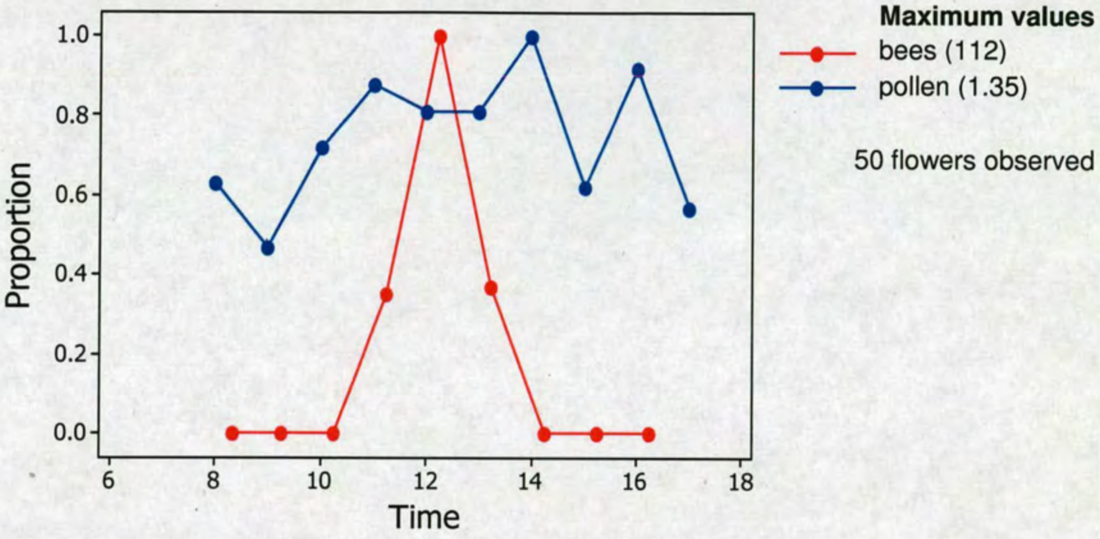

(b) *S. brevispica*, tree 5, 9th June 1999, High Dam

Fig. 5.10 Patterns of pollen availability (blue) and visitation by flies (black) and bees (red) to flower heads of *S. brevispica* (a) tree 6 and (b) tree 5 on 9th June 1999 at High Dam. Data shown are the proportion of the maximum number of visits or amount of pollen available. The figures in brackets indicate the maximum number of visits or pollen to anther ratio.

(a) *V. drepanolobium*, tree 1, 10th September 2004,



(b) *V. drepanolobium*, tree 1, 17th September 2004, Junction

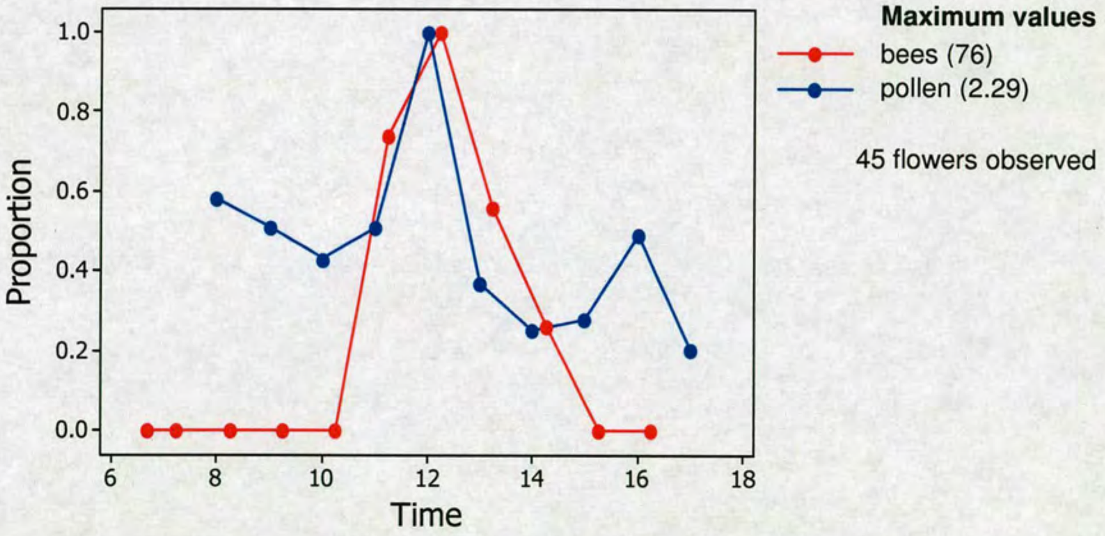
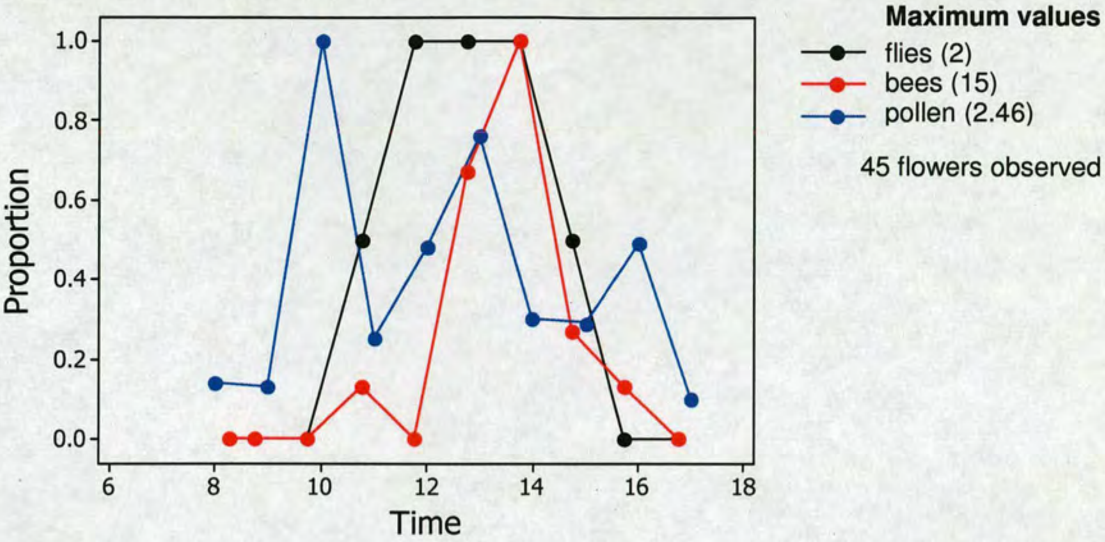
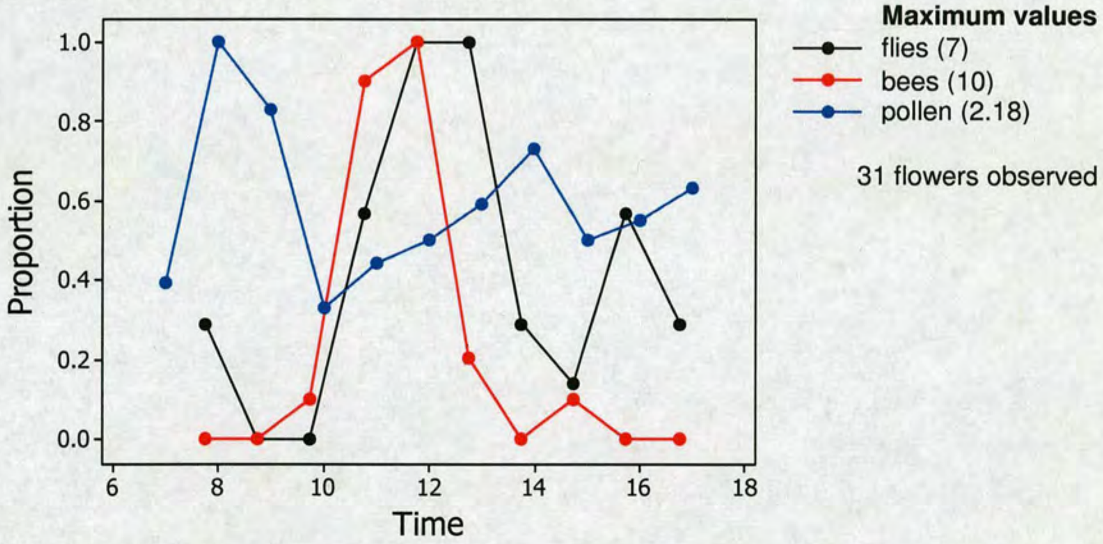


Fig. 5.11 Patterns of pollen availability (blue) and visitation by bees (red) to flower heads of *V. drepanolobium* (a) on 10th September 2004 and (b) 17th September 2004 at Junction. Data shown are the proportion of the maximum number of visits or amount of pollen available. The figures in brackets indicate the maximum number of visits or pollen to anther ratio.

(a) *V. etbaica*, 21st August 2004,



(b) *V. etbaica*, 13th September 2004, Turkana Boma



(c) *V. hockii*, 17th June 1999, High Dam

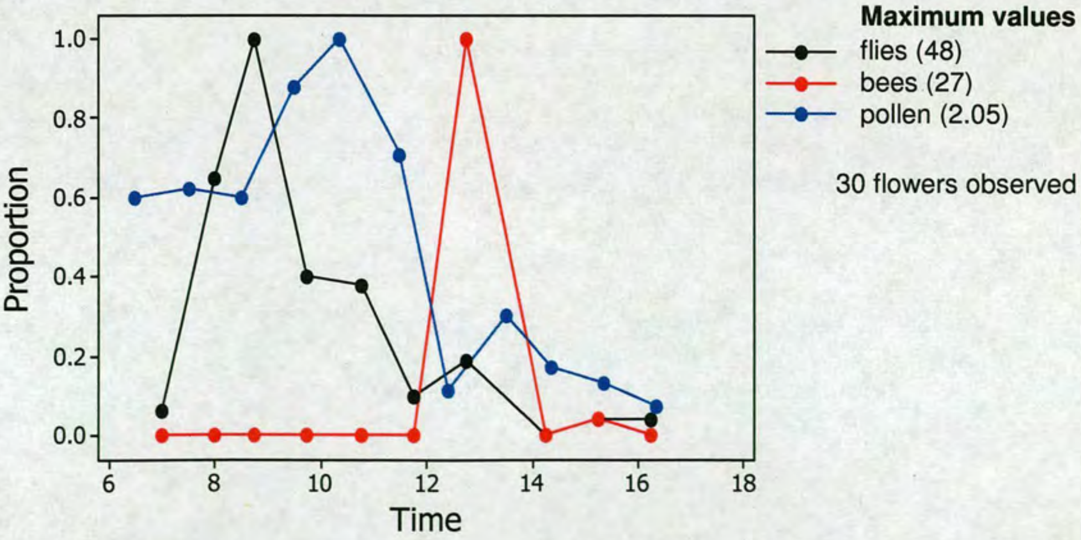
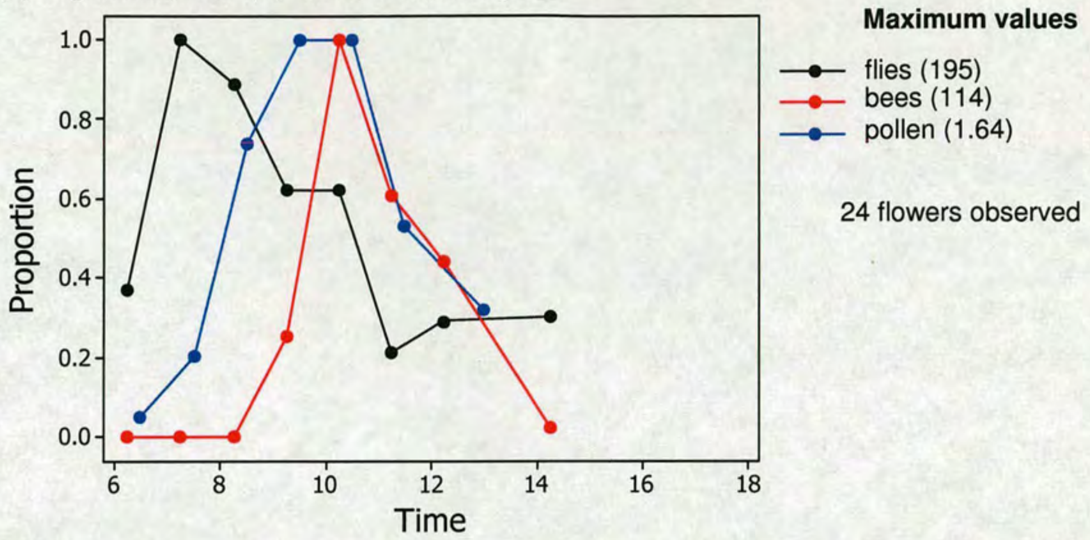
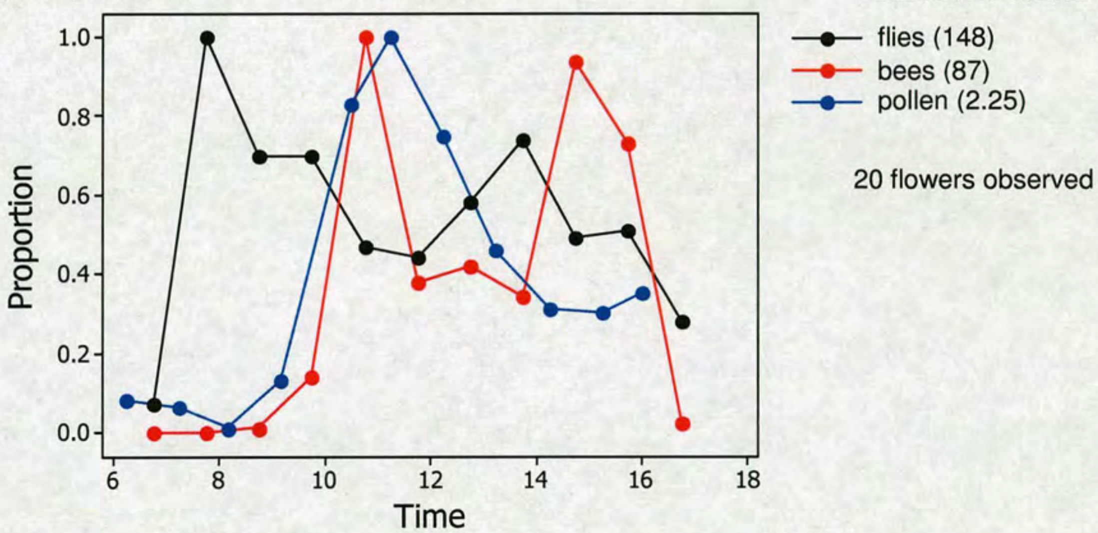


Fig. 5.12 Patterns of pollen availability (blue) and visitation by flies (black) and bees (red) to flower heads of (a) *V. etbaica* on 21st August 2004, (b) *V. etbaica* 13th September 2004 at Turkana Boma and (c) *V. hockii* on 17th June 1999 at High Dam. Data shown are the proportion of the maximum number of visits or amount of pollen available. The figures in brackets indicate the maximum number of visits or pollen to anther ratio.

(a) *V. gerrardii*, tree 1, 6th June 1999, Mongoose



(b) *V. gerrardii*, tree 1, 12th June 1999, Mongoose



(c) *V. gerrardii*, tree 2, 12th June 1999,

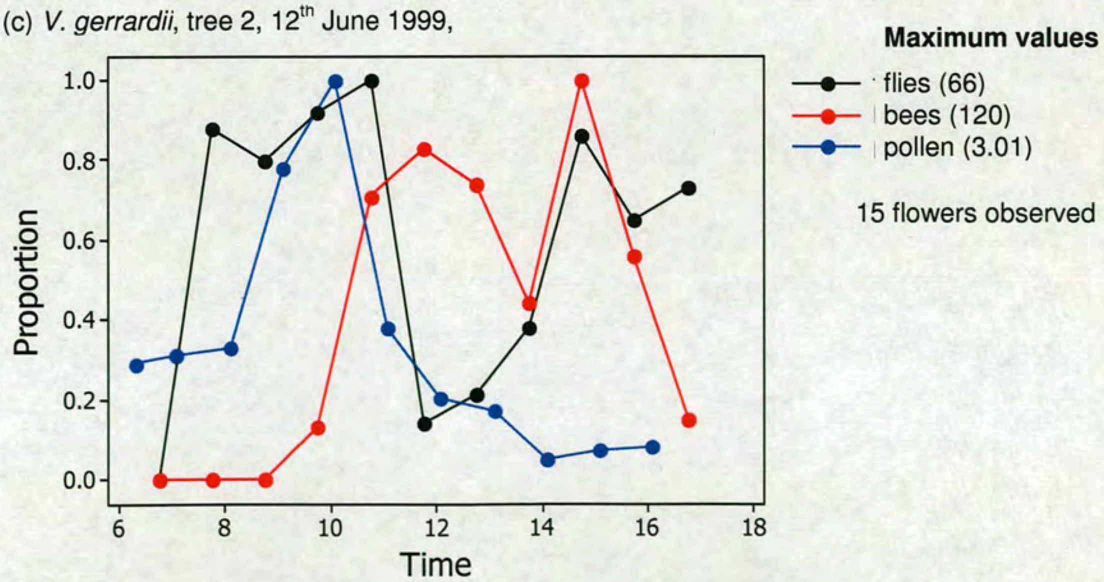
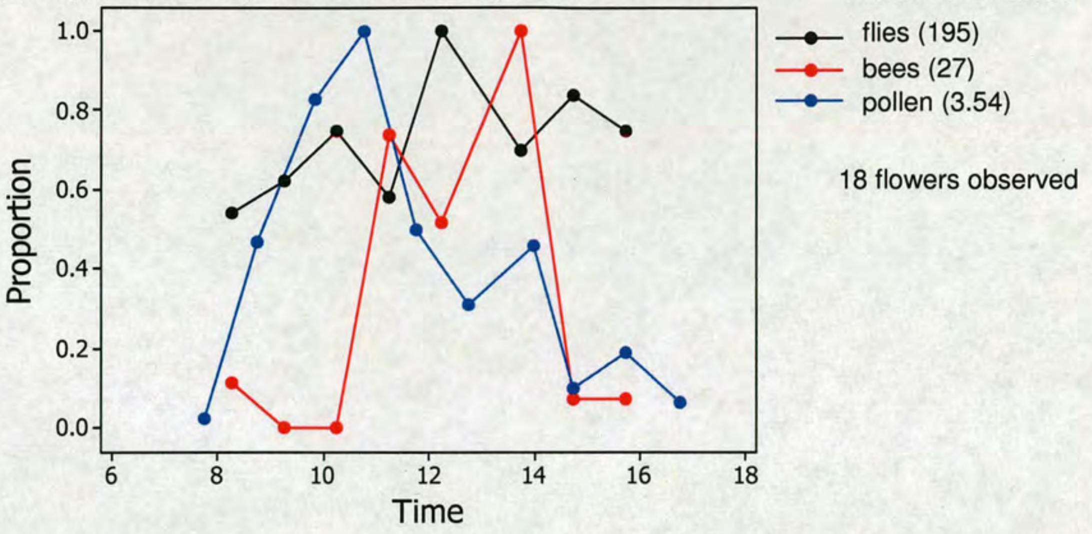
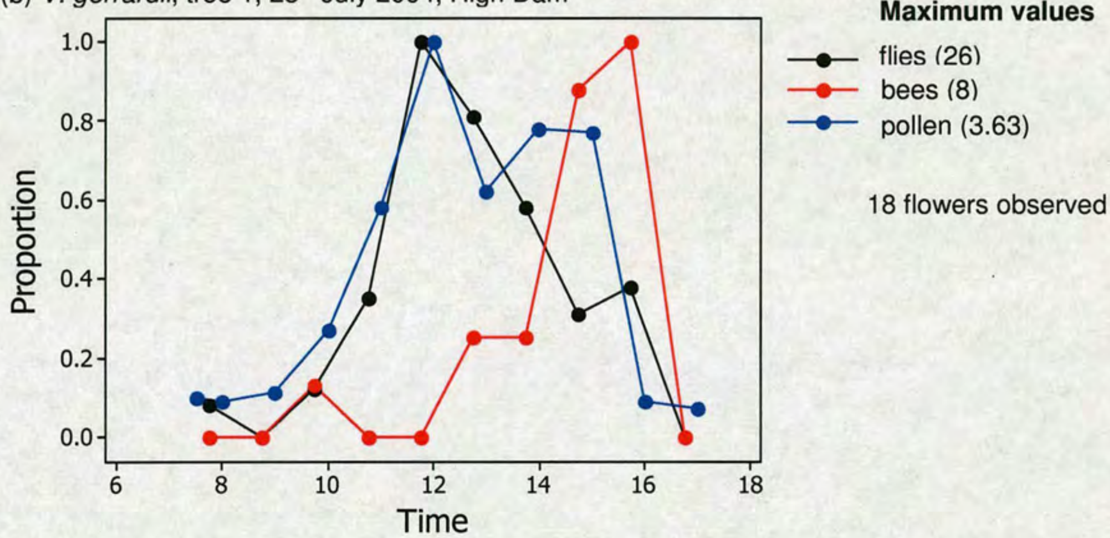


Fig. 5.13 Patterns of pollen availability (blue) and visitation by flies (black) and bees (red) to flower heads of *V. gerrardii* (a) on 6th June 1999, (b) for tree 1 on 12th June 1999 and (c) for tree 2 on 12th June 1999 at Mongoose. Data shown are the proportion of the maximum number of visits or amount of pollen available. The figures in brackets indicate the maximum number of visits or pollen to anther ratio.

(a) *V. gerrardii*, tree 3, 17th June 1999, High Dam



(b) *V. gerrardii*, tree 1, 28th July 2004, High Dam



(c) *V. gerrardii*, tree 2, 28th July 2004, High Dam

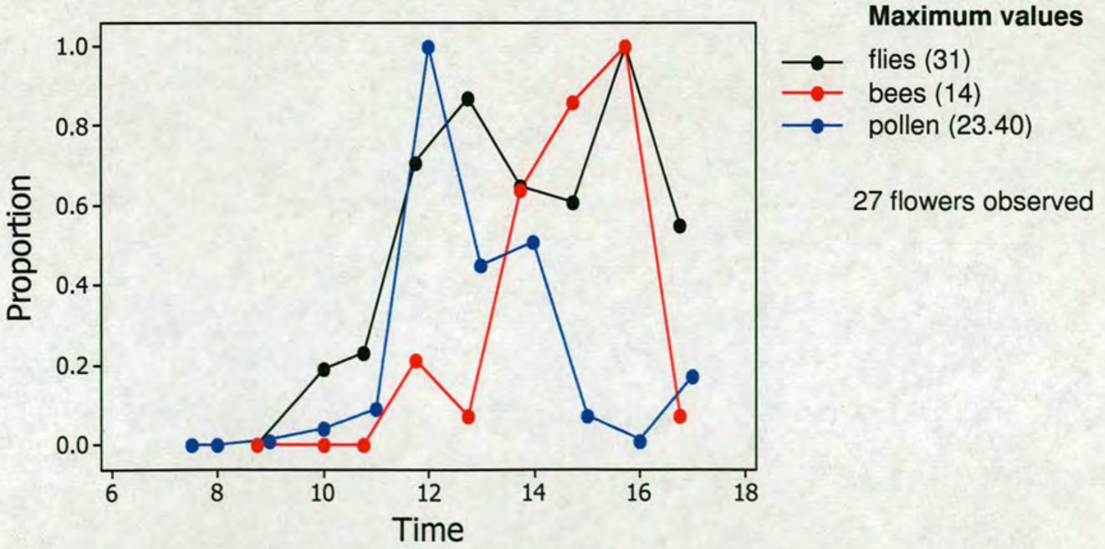
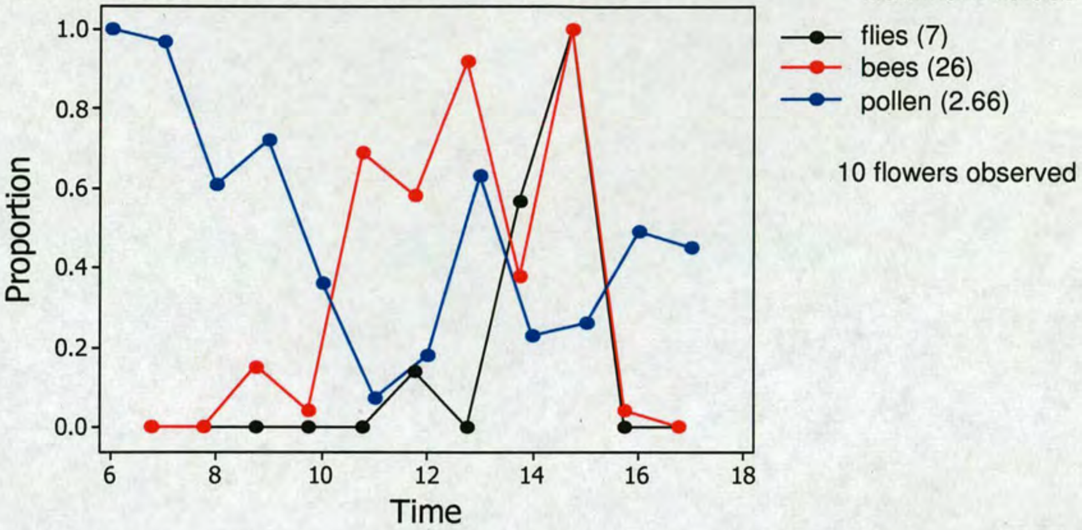
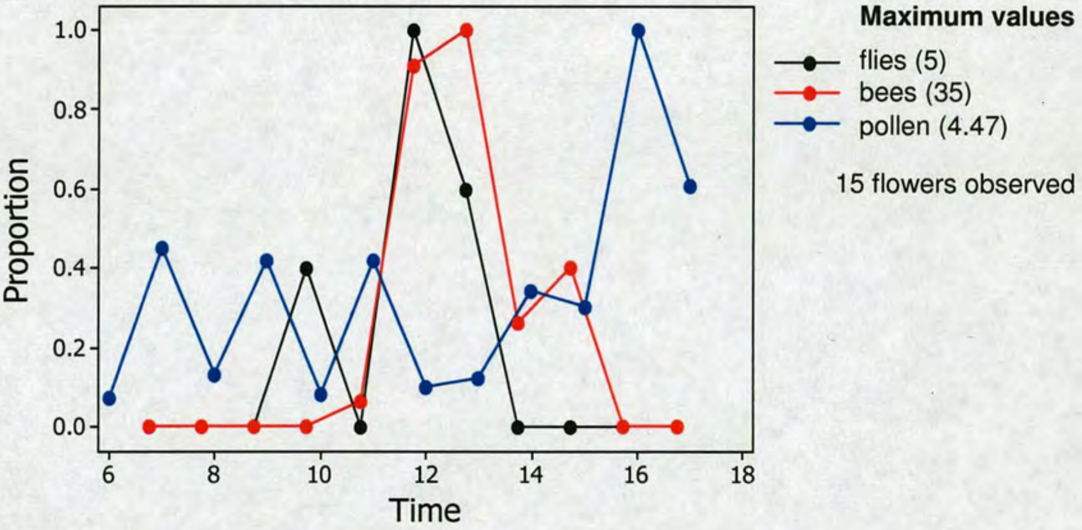


Fig. 5.14 Patterns of pollen availability and visitation to flower heads of *V. gerrardii* (a) on 17th June 1999, (b) for tree 1 on 28th July 2004 and (c) for tree 2 on for tree 2 on 28th July 2004 at High Dam. Data shown are the proportion of the maximum number of visits or amount of pollen available. The figures in brackets indicate the maximum number of visits or pollen to anther ratio.

(a) *V. nilotica*, 21st June 2004, Turkana Boma



(b) *V. nilotica*, 22nd June 2004, Turkana Boma



(c) *V. nilotica*, 16th July 2004, Turkana Boma

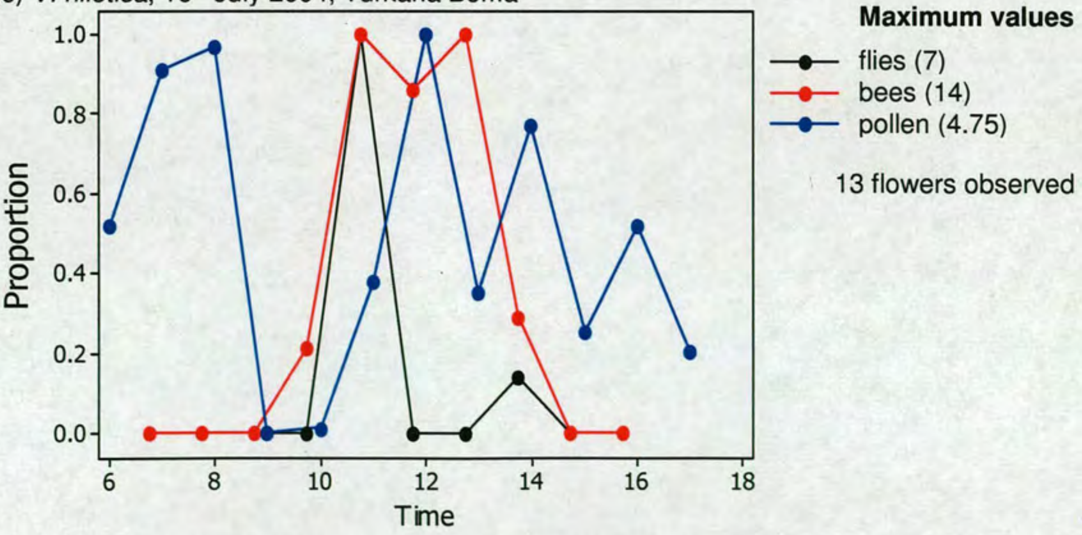
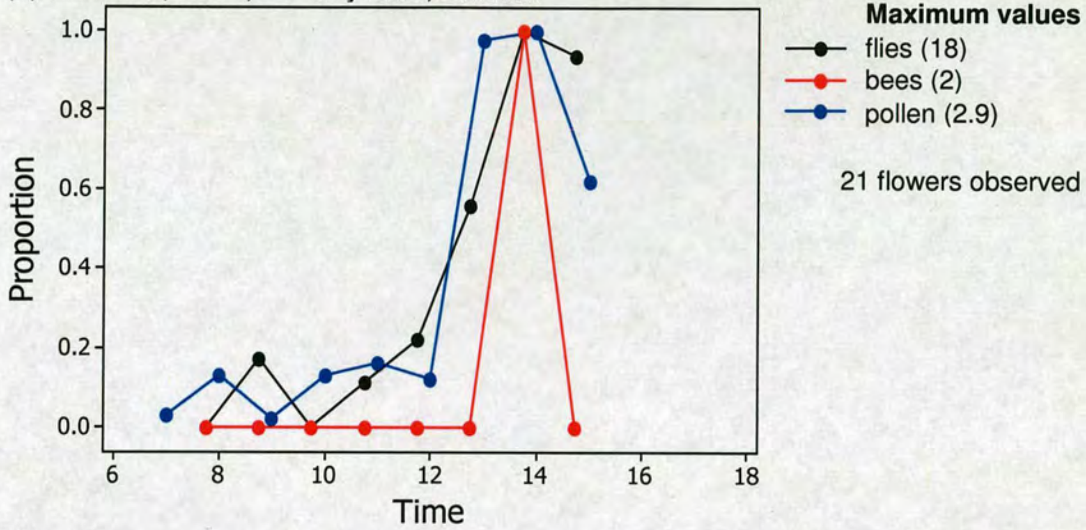
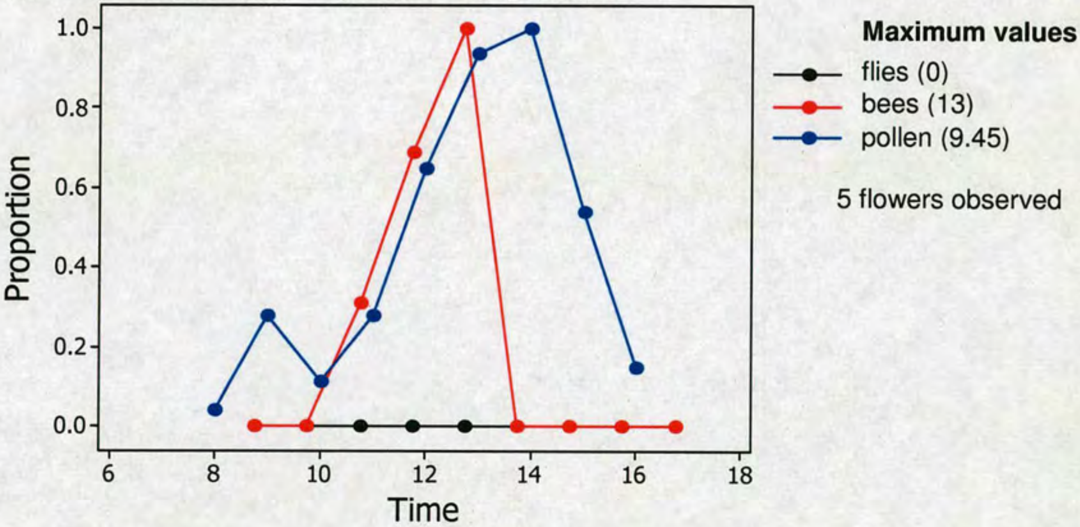


Fig. 5.15 Patterns of pollen availability and visitation to flower heads of *V. nilotica* (a) on 21st June, (b) 22nd June and (c) 16th July 2004 at Turkana Boma. Data shown are the proportion of the maximum number of visits or amount of pollen available. The figures in brackets indicate the maximum number of visits or pollen to anther ratio.

(a) *V. nilotica*, tree 1, 30th July 2004, Junction



(b) *V. nilotica*, tree 1, 10th September 2004, Junction



(c) *V. nilotica*, tree 1, 17th September 2004, Junction

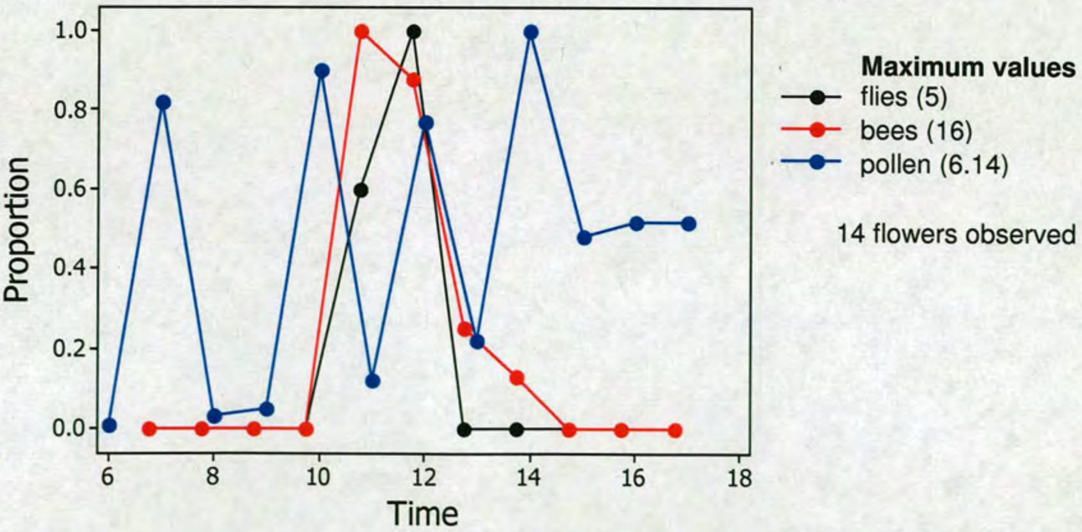


Fig. 5.16 Patterns of pollen availability and visitation to flower heads of *V. nilotica* (a) on 30th July, (b) 10th September and (c) 17th September 2004 at Junction. Data shown are the proportion of the maximum number of visits or amount of pollen available. The figures in brackets indicate the maximum number of visits or pollen to anther ratio.

## 5.4 Discussion

### 5.4.1 Do individual acacia species have characteristic floral visitor assemblages?

The main visitor groups to acacia flower heads at Mpala were flies and bees. The visitor assemblages of *V. drepanolobium*, *V. etbaica*, *S. mellifera* and *V. nilotica* were dominated by bees whilst those of *S. brevispica*, *V. gerrardii* and *V. hockii* comprised large proportions of both bees and flies (Tables 5.4, 5.5). Other visitor groups formed relatively small proportions of the overall visitor assemblages for each species, although wasps were relatively frequent visitors to *S. brevispica* and *V. gerrardii* and Lepidoptera were relatively frequent visitors to *S. brevispica* and *S. mellifera* (Tables 5.4, 5.5).

Most flies were calliphorids or syrphids, although several other fly taxa were observed visiting flower heads (Appendix 6). Fly species commonly caught on acacia flower heads included the calliphorids *Rhyncomya forcipata* and *Chrysomya chloropyga*, the syrphids *Phytomia incisa* and *Eristalinus taeniops* and a newly described species of muscid fly, *Pyrellia acaciae* (Appendix 6). Social bee visitors were *Apis mellifera* and *Plebeina hildebranti*. A wide diversity of solitary bee species visited acacia flower heads. Solitary species captured on flower heads of multiple acacias included megachilid bees in the genus *Megachile*, the apid bees *Macrogalea candida* and *Braunsapis ?bouyssoui*, and a species in the genus *Pseudapis* (Halictidae) (Appendix 6).

The diversity of visitor taxa observed in this study was similar to that recorded by Stone et al. (1996, 1998, 1999a) for an acacia assemblage at Mkomazi in Tanzania. The visitor assemblages for three of the Tanzanian acacias, *V. drepanolobium*, *V. nilotica* and *S. senegal*, were dominated by bees whilst those of *V. tortilis* and *V. zanzibarica* were a mixture of calliphorid flies and bees. The main visitors to *V. drepanolobium* and *V. nilotica* at Mkomazi were megachilid bees in the genus *Megachile*. Tybirk (1989) also recorded *Megachile* as frequent visitors of *V. nilotica* at another site in Kenya. The visitor assemblages for *V. nilotica* at Mpala were similarly dominated by species of *Megachile*. However, most visitors to *V. drepanolobium* during detailed observations at Mpala were *Apis mellifera*, with a much smaller proportion of megachilid bee visits (Table 5.4). The other three acacias sampled at Mkomazi were either not found or not sampled at Mpala, although the visitor assemblages for *V. tortilis* and *V. zanzibarica* at Mkomazi, which were visited by almost equal proportions of bees and calliphorid flies, appeared similar to those for *S. brevispica* and *V. gerrardii* at Mpala.

### 5.4.2 How variable are the floral visitor assemblages for individual acacia species?

The proportions of visits contributed by different taxonomic groups varied among sampling days, between sites and between years in all acacia species. In general, conspecific trees sampled on the same day at the same site had similar visitor assemblages. There were also similarities among conspecific trees sampled at different sites at the same seasonal time for *S. brevispica*, *V. drepanolobium*, *V. etbaica*, *V. gerrardii* and *V. nilotica* (Tables 5.8-5.12). In addition, *V. nilotica* trees sampled at the same seasonal time at Turkana Boma in 2004 and 2005 had very similar visitor assemblages, with *Megachile* forming a large proportion of visits for most trees in both years.

The taxonomic resolution at which visitor assemblages were compared inevitably affected the measured degree of similarity. Overall, there was less variation in visitor assemblages within each acacia species when visitors were grouped at higher taxonomic resolution. Decreases in similarity among visitor assemblages with bees and flies grouped to family reflected different contributions of specific fly and bee taxa to different trees. The abundances of potential visitor taxa are likely to vary in seasonal time so we might expect visitor assemblages to vary over weeks and months, but less so among days close together. However the results from this study indicate that floral visitor assemblages in individual acacia species can vary over periods of just a few days.

### 5.4.3 Do acacias share floral visitors and do their visits represent a significant proportion of all visits?

Ninety-one visitor species were caught on flower heads of multiple acacia species. These included bees, wasps, flies, beetles, butterflies and one species of moth. The potential importance of these shared species as pollinators of each acacia species is unknown since no information on the frequency of visits or the visitation patterns are available for these species. Instead, the proportions of visits contributed by different visitor taxa had to be compared between species at lower taxonomic resolutions.

*Senegalia brevispica* and *V. gerrardii* had the most similar visitor assemblages among all species sampled in each of the 1999 and 2004-5 data sets. The visitor assemblage for *V. hockii* in 1999 was also similar to that of both *S. brevispica* and *V. gerrardii*, although this species was sampled on only one day. All three species had large numbers of visits from flies and bees, and relatively high PS values with these taxa grouped to family level suggest that fly and bee visitor species could have been similar between species. Visitor species caught at flower heads of *S. brevispica* and *V. gerrardii* between 2003 and 2005 incorporated a wide diversity of insect taxa, with 24 visitor species found on flower heads of both species (Appendix 6). Shared visitors incorporated seven bees, six wasps, six flies, three beetles two butterflies and one moth. Although *S. brevispica* and *V. gerrardii* shared specific visitor fauna, the importance of these shared visitors as pollinators is not known for either species.

The visitors to flower heads of *V. drepanolobium*, *V. etbaica*, *V. gerrardii* and *S. mellifera* all included large proportions of bees, meaning that these species had similar visitor assemblages with all visitors grouped at the lower taxonomic level. However, similarity was much lower among these species when flies and bees were grouped at family level. This suggests that bee visitor species varied among these acacias. *Vachellia drepanolobium* was visited mainly by *Apis mellifera*, *V. nilotica* was visited mainly by *Megachile* species and *V. etbaica* and *S. mellifera* were visited mainly by megachilid and apid bees, including *Apis mellifera* (Table 5.4). Of the identified visitor species caught on acacia flower heads, 41 were caught on more than one of these acacias (Appendix 6). This shows that visitor species were shared among these four acacias over seasonal time, although the proportions of visits and the relative importance of shared taxa are not known.

Although many insect taxa visited acacia flower heads, not all will be effective pollinators. The most effective will be those that frequently visit flower heads of the same acacia species, move between individual trees of the same species and carry pollen that is available for transfer between flower heads. Bees and flies visited acacias in the largest numbers. Most bees moved rapidly between flower heads and trees, although their fidelity to a single acacia species at this location is not known. The behaviour of flies on flower heads varied among taxa. Syrphids and bombyliids moved rapidly between flower heads and trees. Some calliphorids, muscids and sarcophagids moved between trees, although many remained on individual flower heads for long periods or moved among flower heads on individual trees. Flies ingest pollen that they collect, although it is likely that pollen will be deposited on their bodies as they forage on flower heads.

Most previous studies have considered bees to be more effective pollinators of acacias than flies (Tybirk 1989, Stone et al. 1998). All the acacias in this study were visited by bees. Although the relative proportions of visits by different bee taxa varied among acacia species, the capture data suggest that all were visited by a wide range of bee species. Seven bee species were captured on flower heads of at least five of the acacias sampled. These included apid, halictid and megachilid bees (Appendix 6). However, since the relative proportions of visits to different acacia species for each of these bee species is not known, it is difficult to assess their potential as pollinators.

### 5.4.4 Do daily patterns of visitation vary within and between acacia species?

Daily patterns of visitation to flower heads varied across days for all acacia species examined. Peak visitation rates occurred for all species between 8.30 and 16.00 and varied over a period of between 2.5 and 6 hours in each species (Table 5.24, Fig 5.1). The range of times over which peak visitation occurred overlapped among all species although overlapped least for *S. brevispica* and *V. drepanolobium*. The peak visitation rate for *V. hockii* occurred much earlier than for other species, although the peak bee visitation rate corresponded more closely to peak visitation in other acacias. Flies and bees had different patterns of visitation to flower heads, with flies active much earlier in the day than bees. On most trees, visitation rates for flies peaked earlier than those for bees.

Co-flowering acacia species with peak visitation rates at similar times of day might compete for shared pollinators. The most commonly co-flowering group of acacias at Mpala was *S. brevispica*, *V. drepanolobium*, *V. gerrardii*, *V. nilotica* and *V. seyal*. Visitor assemblages and daily patterns of visitation were sampled in this study for all except *V. seyal*. *Senegalia brevispica* and *V. gerrardii* were visited mainly by flies and bees, whereas *V. drepanolobium* and *V. nilotica* were visited mainly by bees. Bees are generally considered to be more effective pollinators for acacias, although some fly taxa, especially syrphids, are likely to be effective pollinators. The times at which peak bee activity was observed across days was similar among these four acacias (Table 5.24). However, climatic variation between days could affect the timing of bee activity, and peaks for different acacias might occur at different times on the same day. There were few days in this study on which multiple acacia species were observed for floral visitors. *Vachellia drepanolobium* and *V. nilotica* were both observed on 10th September and 17th September 2004 at Junction and visitation rates peaked at similar times for both species on each day (Figs. 5.4, 5.8). The visitor assemblages were very different on 10th September, with *V. drepanolobium* visited mainly by *Apis mellifera*, and *V. nilotica* visited mainly by *Megachile*, with additional visits from apid bees (Tables 5.19, 5.21). However, on 17th September the visitor assemblages for the two species overlapped considerably more, with apid bees and *Megachile* forming a larger proportion of overall visits to *V. drepanolobium*.

Whilst the bee visitor assemblages for the co-flowering species differed between sites, and in daily and seasonal time, the capture data highlight that all potentially shared bee and some syrphid fly pollinators. Considering this along with the overlapping peak visitation times, it seems that the co-flowering acacias at Mpala have the potential to compete for pollinators.

In the Tanzanian study, megachilid bees dominated flower head visits for two of five co-flowering acacia species and formed a smaller proportion of total visits for the other three (Stone et al. 1998). At Mpala, *Megachile* were the dominant bee visitors for *V. nilotica* trees at Turkana Boma. Megachilids, most of which were *Megachile*, formed approximately 40% of bee visits in *S. brevispica* and *V. gerrardii* in 2004-5 (Table 5.4) whereas *V. drepanolobium* was visited much less frequently by

*Megachile*. All acacias at Mpala were visited by a wide range of bee taxa and there were no species that appeared to dominate flower head visits in multiple acacia species.

In contrast to the acacias at Mkomazi, most of the co-flowering acacias at Mpala flowered over long periods of time, and perhaps cannot rely on limited groups of pollinators. The generalised visitor assemblages at Mpala suggest that different bee species might act as effective pollinators at different seasonal times, although it is not clear to what extent these pollinators might be shared among co-flowering acacias.

*Senegalia mellifera* and *V. etbaica* co-flowered less often with other acacias. These species mass flower at particular seasonal times with many trees producing large numbers of flower heads simultaneously. This strategy might enable them to outcompete other floral resources during the short periods over which they flower and attract sufficient pollinators. Field observations noted that both species attracted large numbers of visits from *Apis mellifera* and *Plebeina hildebranti* when in mass flower, with *S. mellifera* flower heads also visited in large numbers by *Megachile* species.

### 5.4.5 Do patterns of visitation track patterns of pollen availability in each acacia species?

Visitation patterns for the main visitor groups corresponded to patterns of pollen availability in all species. In general, the peak visitation rates for bees corresponded more closely to increased levels of pollen availability than that of flies. Fly visitation rates peaked prior to maximum pollen availability in several species, although were more synchronous with pollen availability peaks for others.

These results suggest that patterns of visitation to flower heads were determined by the availability of pollen, with increased visitation rates at times when pollen availability was high. This was particularly so for bees, whose activity at flower heads was closely linked to high levels of pollen availability.

The tracking of pollen availability by visitors to flower heads demonstrates that a potential mechanism exists by which shared pollinators could be structured in daily time, as for the acacias at Mkomazi. However, the times at which pollen availability peaked in each species were extremely variable and were not regularly spaced in daily time (Chapter 4); therefore it is unlikely that pollinators are structured in daily time at Mpala in the same way as they were at Mkomazi. At Mpala, flowering occurs over longer seasonal time periods than at Mkomazi, and species' flowering peaks do not occur simultaneously. Since pollination takes place over a longer seasonal time at Mpala, competition for pollination could be less intense meaning that no process to drive the divergence of pollen release in daily time exists for co-flowering acacias at Mpala. Furthermore, if daily nesting cycles and thermal physiology requirements for important bee pollinators dictate the times of day at which they can forage, even if competition for pollination does exist, it could be more advantageous for acacia species to retain their timing of pollen release at a time of day that is optimal for pollinator visits, than to diverge in daily time to reduce the potential of heterospecific pollen transfer.

### 5.4.6 Further studies

The findings in this chapter demonstrate that visitor species to flower heads are shared among species, and that visitation of shared pollinator groups overlaps in daily time among acacias. However, the importance of these shared visitors as pollinators for each acacia, and whether visitors are shared on the same day, or even at the same time of year, cannot be determined from this study.

To ascertain whether shared visitor species are important pollinators, information regarding (i) the frequency of their visits to flower heads, (ii) their patterns of movement among trees of the same species, and (iii) between different acacias (i.e. their level of floral constancy) is needed.

Visitor identification, particularly for rapidly moving species, can be difficult when the observer is at a far enough distance away from a tree to minimise the disturbance to visitors on flower heads. Therefore quantification of visits to flower heads in this study was limited to broader taxonomic groups supplemented with additional information gained from catching visitors at other times. Familiarity with the visitor species could improve the level of identification achieved in such studies and allow the comparisons of assemblages and daily visitation patterns at the level of visitor species.

Whilst visitor movement between trees can be difficult to track (but see the use of fluorescent dye in Raine 2001), some information on a visitor's floral constancy and its potential ability to transfer pollen for a particular plant species can be obtained from examining pollen loads. For bees, examination of pollen carried in the scopae can reveal the plant species on which an individual has been recently foraging. For other taxa, pollen carried on the surface of the body can show recent foraging histories.

To be able to draw more accurate conclusions regarding the extent to which co-flowering acacias share visitors in daily time at Mpala, all co-flowering species should be examined over a relatively short timescale and at the same site. This would require a large team of observers familiar with the visitor fauna.

# Chapter 6. Community-level analyses of plant-visitor interactions

## Summary

Two flowering plant communities at Mpala were sampled for flower visitors over four months. Flower-visitor interaction webs were constructed for each month at each site. In all webs bees made the most visits and had the highest species and interaction diversities. Other flower visitors were wasps, ants, flies, beetles, bugs, butterflies and moths. Although individual visitor species were present across seasonal webs at a single site, they rarely visited the same plant species at different seasonal times. This is compatible with partitioning of pollinators across seasonal time, however more detailed studies would be required to determine whether this is the case, or if interactions were missed due to the low resolution of sampling for each plant species.

Flower-visitor interactions were compared across four daily time periods: 6.00-9.00, 9.00-12.00, 12.00-15.00 and 15.00-18.00. All plant species with open flowers were observed in each time period. Comparisons with randomised interaction webs generated using null models showed that the number of interaction types in each time period was significantly lower than expected in all seasonal webs. This suggests that interactions were structured in daily time. Evidence for bottom-up control of daily temporal structure was shown through the restricted opening times of some plant species.

Plants shared visitor species within and across time periods in all seasonal webs and acacias shared visitors with a wide range of plant species in several webs. Plants sharing visitors across time periods could be partitioning visitors in daily time, however more detailed investigations are required. Further studies to examine whether daily temporal structure in these communities is controlled by bottom-up effects of the timing of reward presentation or top-down effects of pollinator activity are discussed.

## 6.1 Introduction

So far in this thesis I have looked for evidence of pollinator partitioning in daily time within an acacia species assemblage. Although groups of acacia species do co-flower at Mpala (Chapter 3), and some floral visitors are shared among species (Chapter 5), there is little evidence to suggest that acacia species partition visits in daily time. Although there is some variation in the daily timing of pollen release (Chapter 4) and visitation (Chapter 5) across acacia species, there is no evidence that either are structured among co-flowering species.

Failure to detect temporal structure could be due to (a) a genuine absence of structure or (b) involvement in structuring interactions with plants other than acacias. As well as pollinator sharing occurring among closely related groups of species, it is entirely plausible that pollinators might be shared among a broader diversity of plants. The flowering plant community at Mpala contains a much wider community of plant species than the acacias and given that acacia flower heads are accessible to a wide range of visitor species, it is likely that these visitor species might utilise resources from other plant species in the community. In this chapter I examine two flowering plant communities at Mpala for evidence of daily temporal structure among plant-visitor interactions.

### 6.1.1 Why should studies consider daily temporal variation in plant-pollinator communities?

Interactions between plants and pollinators are known to vary on daily temporal timescales (e.g. Armbruster and Herzig 1984, Herrera 1990, Stone et al. 1996, 1998, Raine 2001, Willmer and Stone 2004, Kajobe and Echazarreta 2005). Pollinators commonly visit specific plant species within a characteristic time window each day, determined by the interaction between pollinator physiology, daily cycles of microclimate, and the availability of floral rewards (Herrera 1990, Willmer and Stone 2004). Daily activity patterns for bees have been well documented (reviewed in Willmer and Stone 2004). Larger bee species generally have greater thermoregulatory abilities than smaller bees and can initiate flight activity at lower ambient temperatures than smaller bees (reviewed in Willmer and Stone 2004). However, smaller bees can commonly maintain greater activity at higher temperatures, since large bees are more likely to overheat. Therefore large bees, such as bumblebees (*Bombus*, Apidae) and large anthophorid species (Apidae, tribe Anthophorini) typically show bimodal activity patterns, with peaks early in the morning and later in the day when temperatures are cooler (Linsley 1978, Herrera 1990, Stone 1994, Willmer and Stone 1997b, Stone et al. 1999b). In contrast, smaller bee species are often active throughout the day, with a single activity peak (Linsley 1978, Herrera 1990, Minckley et al. 1994, Willmer and Stone 1997b, Biesmeijer and Toth 1998). Nesting cycles will also affect bee foraging patterns (reviewed in Willmer and Stone 2004). Solitary female bees can usually construct one new cell per day, and divide their time between initiating, provisioning and closing cells, as well as collecting nectar for themselves (e.g. Willmer and Stone 1989). Therefore foraging activity can be restricted by nest provisioning requirements, and females are likely to seek different floral rewards at different times of day. In contrast, in social species, activities in the nest can be carried out by different subsets of the worker population and the foraging patterns of female worker bees are likely to be less restricted (Willmer and Stone 2004).

Less is known about the daily foraging patterns of other pollinator taxa. The foraging activities of many taxa have been linked to climatic variables such as temperature (Willmer 1983, Corbet 1990, Herrera 1995a, 1995b) and solar irradiance (McCall and Primack 1992, Herrera 1995b). Daily activity has been shown to be temperature dependent in the sphecid wasps *Philanthus triangulum* (Strohm and Linsenmair 1998) and *Cerceris arenaria* (Willmer 1985). Peng et al. (1992) found that both temperature and wind speed affected the daily abundance of various dipteran taxa. Both solar irradiance and temperature were found to limit the foraging activity of *Usia aurata* (Bombyliidae) on *Calendula arvensis* inflorescences (Asteraceae) (Orueta 2002). Willmer (1982) found that two species of *Sarcophaga* (Sarcophagidae) are able to thermoregulate, which allows them to forage on flowers for longer than competitors. Stone et al. (1988) showed that the foraging activities of two papilionid butterflies were primarily determined by temperature, but also affected by nectar supply.

While the causes and consequences of daily temporal structure have been widely studied in specific pollination mutualisms (e.g. Stone et al. 1998, Herrera

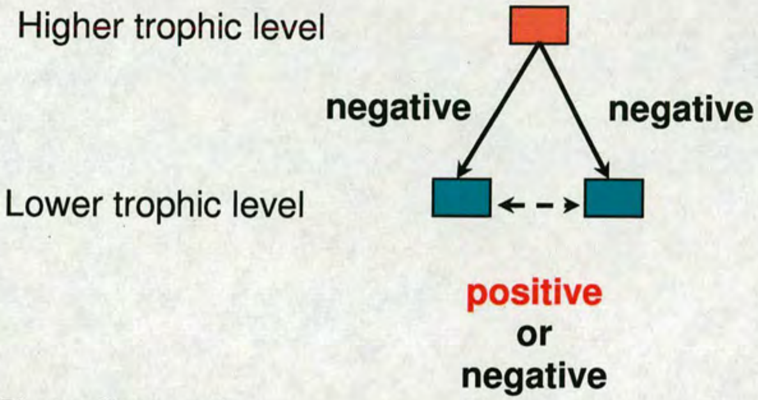
1990, Herrera 1995a, 1995b), the potential for such structure in multi-species interactions linking whole communities of plants and pollinators remains unstudied. The potential significance of daily temporal structure has grown with the realisation that co-flowering plant species commonly share pollinators (Waser et al. 1996, Bronstein et al. 2006, Thompson 2006, Waser and Ollerton 2006). The impact of shared pollinators depends on the temporal patterning of their activity. If shared pollinators visit co-flowering plants simultaneously, these plants may compete for the quantity and/or quality of pollinator visits. In contrast, if shared pollinators visit specific plants at specific times of day, then competition for pollination can be avoided, and co-flowering plants could potentially facilitate each other's reproduction through the maintenance of larger pollinator populations than could be sustained by any single plant species. These alternative scenarios have very different predictions for the impact of disturbance to the complex webs of interactions that link plants and pollinators in natural communities.

### 6.1.2 Community level interaction webs

Relationships within communities of interacting species at different trophic levels have traditionally been represented using food webs (Pimm et al. 1991, Polis and Winemiller 1996, Pimm 2002). Interaction webs (also referred to as networks) can also be used to represent mutualistic relationships within communities, such as those between plants and their pollinators or seed dispersers (Jordano 1987, Memmott 1999, Thompson 2006).

Since the construction of the first plant-pollinator web for a British meadow community (Memmott 1999), community-level pollination studies have increasingly incorporated this approach in the examination of relationships among groups of plants and their pollinators (e.g. Dupont et al. 2003, Hegland and Totland 2005, Lundgren and Olesen 2005, Basilio et al. 2006, Morales and Aizen 2006, Stang et al. 2006).

(a) Food web (e.g. predator-prey or host-parasitoid)



(b) Plant-pollinator web

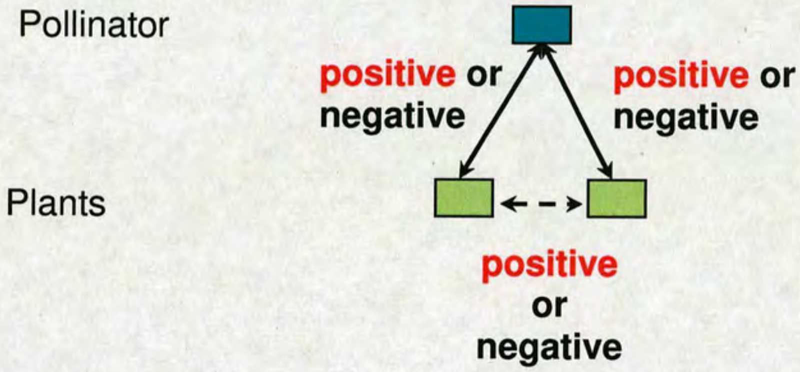


Figure 6.1 Schematic diagrams to show the types of interactions that occur among species in (a) food webs and (b) plant-pollinator webs.

Whilst community pollination studies have been able to build on the knowledge obtained during many years of food web study, interactions between plants and their pollinators are fundamentally different to those that exist between species at different trophic levels in food webs. In food webs, species at higher trophic levels have negative direct impacts on those at lower trophic levels (see Fig. 6.1). For example, predators will negatively affect prey species and parasitoids will negatively affect host species. In contrast, in plant-pollinator webs the interaction between plant and pollinator species is usually positive for both groups. However, direct interactions can be negative if visitors rob rewards and do not pollinate, or if they deposit incompatible pollen. In addition, in both types of web, species within trophic levels can indirectly affect one another negatively through apparent competition or positively through facilitation. In food webs, an abundant prey species can have an indirect negative effect on other prey species by causing an overall increase in predators. If these predators then switch to alternative prey species, they can mediate apparent competition between alternative prey (Holt and Lawton 1994, Abrams et al. 1996, 1998). Alternatively, if a predator preferentially targets a competitively superior prey species, this can result in competitive release for a less dominant prey species (Abrams and Matsuda 1996, Abrams et al. 1996, 1998). In plant-pollinator webs, plants can interact negatively by competing for pollinators or interact positively by facilitating pollination for one another. Facilitation here is analogous to apparent competition in trophic webs, except that shared pollinators are beneficial rather than detrimental. Consideration of the timescale over which species interact can influence whether interactions are interpreted as positive or negative for interacting species.

The type of web that can be constructed for groups of plants and pollinators depends on the amount of information available regarding the interactions between them. Flower-visitor webs are used to represent communities in which only the identities of flower visitors have been recorded. These webs have been more commonly used as it is relatively easy to collect data on flower visitors (e.g. Dicks et al. 2002, Memmott and Waser 2002). However, whilst these webs can demonstrate potential pollinator species, they cannot confirm whether flower visitors are effective pollinators, since nothing is known about their ability to transfer pollen among different plants of the same species. A second type of plant-pollinator web incorporates data on the pollen loads carried by flower visitors. Pollen transport webs show which flower visitors carry the pollen grains of which plant species (e.g. Forup and Memmott 2005, Gibson et al. 2006). These webs give a more accurate indication of flower visitors that could be acting as successful pollinators. Both types of webs can be qualitative or quantitative. Qualitative webs show the presence of links between interacting species whereas quantitative webs incorporate information on the relative abundance of plant and visitor species, and the frequency of interactions between them. Interaction frequency has been shown to be a useful indicator of the relative importance of flower visitors as pollinators for plant species (Vazquez et al.

2005a), therefore quantitative webs are a more effective approach for investigating the links between plant species and potential pollinators in communities.

### 6.1.3 Temporal variation in community-level pollination studies

The recognition of pollination as a crucial ecosystem service has lead to a growing number of pollination studies that examine entire flower-visitor communities. Whilst such studies are invaluable for identifying potential links among important species in a community, webs summarising interactions observed over long time periods risk losing important patterns in the specific timings of interactions over both seasonal (Waser et al. 1996, Basilio et al. 2006) and daily timescales (Waser et al. 1996). Plant species that appear to be competing for the same pollinator species in a summarised interaction web might be visited at different daily times, and could in fact facilitate pollination for one another.

Although several studies have recognised that interaction webs can only be representative of a limited time period and that plant-visitor interactions cannot be pooled over long periods of time (Dupont et al. 2003, Petanidou and Lamborn 2005, Morales and Aizen 2006), very few have incorporated seasonal temporal variation (Lundgren and Olesen 2005, Basilio et al. 2006). Despite abundant evidence to show that individual pollinators show daily patterns in their activity, no studies to date have considered the structure that could exist on a daily temporal timescale within plant-pollinator communities.

### 6.1.4 Examining the structure of interaction webs

The analysis of multi-species data collected in a field environment for the presence of a specific pattern or structure can be complicated by the fact that the composition of the community in the absence of that pattern is usually unknown. Null model analyses have been widely used in the field of community ecology to attempt to circumvent this problem. Null models are statistical tests widely used in ecology and biogeography that deliberately exclude a mechanism of interest, and allow for randomisation tests of ecological data (Gotelli and Graves 1996, Gotelli 2001). A typical null model randomly generates communities expected to occur in the absence of a particular mechanism and then an index of community structure for the observed data can be compared to the distribution of the same values from the randomly generated communities (Gotelli and Graves 1996). The position of the observed index in the tails of this null distribution can be used to assign a probability value to the pattern as in a conventional statistical analysis (Gotelli and Graves 1996). Although null models can reveal unusual patterns in ecological data, they cannot identify the mechanism responsible for such patterns (Gotelli and Graves 1996).

Null models have been applied to many aspects of food web theory (e.g. Kenny and Loehle 1991, Pianka 1994, Melian and Bascompte 2004, Prado and Lewinsohn 2004, Bascompte and Melian 2005, Vazquez et al. 2005b). Recently, null models have also been used to investigate the structure of plant-animal mutualistic webs, in particular patterns of specialisation and the nested structures of interactions (Bascompte et al. 2003, Vazquez and Aizen 2003, 2004, 2006, Vazquez 2005, Fortuna and Bascompte 2006, Jordano et al. 2006, Lewinsohn et al. 2006), and the effect of extinction and stability on these networks (Memmott et al. 2004, Fortuna and Bascompte 2006). These studies have found that mutualistic interaction networks are usually nested, with asymmetric patterns of specialization, i.e. that highly specialised species tend to interact with more generalised species (Bascompte et al. 2003, Vazquez and Aizen 2004, 2006, Jordano et al. 2006).

In this chapter I use null model analyses to examine observed patterns of interactions among plant and visitor species for daily temporal structure. The methods are described in Section 6.2.5.

### 6.1.5 Daily temporal structure in savannah plant-visitor communities

In this chapter I examine flower-visitor interaction webs at Mpala for daily temporal structure using multiple data sets collected at several seasonal time periods at the same two sites (Turkana Boma and Junction). For each web, the flower-visitor interactions in four daily time periods were compared with null model predictions (see Section 6.2.5) to assess the evidence for significant daily temporal structure. Flower visitors found on multiple plant species were compared across time periods to examine the potential for daily temporal partitioning of shared pollinators among plant species. I also examine whether acacia species at Mpala share visitors with other plant species in the communities, and whether there is any evidence to suggest that acacia visitors are partitioned in daily time among acacias and other plant species.

Specifically, I address the following questions:

1. To what extent do visitors, plants and their interactions change across seasonal time, and are these patterns consistent across sites?

2. Within each seasonal web, to what extent are interactions structured in daily time?

3. Do plant species share visitors, and how are interactions of shared visitor species patterned through time?

4. To what extent do acacias share visitors with other plants and how are interactions of shared visitor species with other plants patterned through time?

5. How do daily time periods differ climatically and are climatic differences across time periods correlated with variation in the visitors active in each time period?

## 6.2 Methods

### 6.2.1 Study sites and dates

Data allowing construction of quantitative flower-visitor interaction webs were collected at Turkana Boma between 4th May and 31st August 2004, and at Junction site between 2nd June and 23rd July 2004 (see Chapter 2 for further details of these sites). Sampling for each flower-visitor web was carried out over two weeks. A complete data set was collected for each week and these were combined to construct a single web. Two weeks represents the minimum time over which sufficient data could be collected and I am assuming that this is a short enough timespan to allow summation of data without major impacts of changes in climate or species diversity. There was at least a two week gap between data collection for consecutive webs.

Four flower-visitor webs were constructed for the Turkana Boma site, one each for data collected in May, June, July and August 2004. The August web was constructed from only one set of data due to time limitations in the field. There were a large number of species flowering at this site during this month, and it took two weeks to conduct the first set of observations for these species. Therefore a second set of data could not be collected within the required time limit. Two webs were constructed for the Junction site, one each for data collected in June and July 2004. In months when both sites were sampled, data were collected simultaneously at each site in order to minimise differences that could have arisen from differing climatic conditions over seasonal time.

I was assisted by Dr G. N. Stone and R. Eraguy in data collection for this chapter.

### 6.2.2 Data collection

*(a) Quantification of floral abundance for each plant species*

A 0.5 ha. (100m x 50m) plot was marked at each site. At the start of a sampling week all flowering plant species were identified in each plot and the number of flowers of each species were quantified. Since floral morphology can differ between species, in order to ensure consistency throughout the study a floral unit was defined for each plant species. This was defined following Gibson et al.

(2006) as an individual flower or collection of flowers that an insect of approximately 0.5 cm could walk within or fly between. For most species this measure was relatively simple to define and floral units were counted at the level of the individual flower. For plant species with composite flower heads, such as those in the family Asteraceae or subfamily Mimosoideae (acacias), a flower head or inflorescence containing a number of individual flowers or florets was classed as a single floral unit.

Flower opening times varied among plant species and few species were open for the entire day. Floral abundance surveys were conducted between 10.00 and 13.00 as the flowers of most plant species were open during these hours. It was sometimes necessary to revisit at an alternative time to obtain an accurate measure of floral abundance for species that closed early or opened late in the day (e.g. species of *Commelina*, *Sida*, *Melhania* and *Ipomoea*).

Most plant species were identified to species level by Professor A. Schnabel using keys and descriptions in Blundell (1992) and Agnew and Agnew (1994). It was not possible to determine an exact species name for some plants so these were recorded as *Genus* sp. and were numbered if there was more than one unidentified species in that genus. There were two species of *Commelina* (Commelinaceae) with blue-lilac petals at Turkana Boma; *Commelina erecta* and *Commelina benghalensis*. These were not separated during the study and were grouped as '*Commelina* spp. blue'. Both species flowered at the same seasonal times and had flowers that were open at similar times of day. Two similar-looking species in the Asteraceae with yellow flowers, *Emilia discifolia* and *Osteospermum vaillanti*, were not identified during the May web at Turkana Boma and were grouped as 'Asteraceae spp. yellow'. Woody shrubs in the genus *Grewia* (family Tiliaceae) flowered at both sites during the study. These were grouped as *Grewia* spp. as individual species were not identified. However, few observations of these plants were made as few flowers occurred at any one time. Twelve species (six per site), each of which occurred in only one month of the study, could not be identified and are referred to as unknown sp. 1, sp. 2, etc.

*(b) Observations for flower visitors*

In the week following the floral abundance survey I attempted to quantify floral visitation to all plant species flowering in each plot. It was not always possible to observe all of the species during weeks with a high diversity of flowering plant species. In these weeks plant species were selected for observation based on their abundance. Species that were not observed were excluded for the following reasons: (i) their abundance in the plot was low with fewer than ten floral units, (ii) flowering was limited to a single individual with fewer than 40 flowers, (iii) the amount of flowering decreased during the week resulting in insufficient flowers for observation. On average 73% of the flowering plant species in a plot were observed for each web. If a plant species began flowering after the floral abundance survey had been conducted, it was observed if there was sufficient time remaining for it to be included in sampling.

Observations were conducted between 6.00 and 18.00 (approximately dawn to dusk). Each plant species received four 20 minute observations per week, one in each of the following time periods: (i) 6.00-9.00, (ii) 9.00-12.00, (iii) 12.00-15.00 and (iv) 15.00-18.00. No observation was made if the flowers of a particular plant species were closed during an entire three hour time period. If the flowers of a plant species were open for a portion of the time period, every effort was made to sample the species whilst it was open. Ideally observations would have allowed for night-visiting species and included the period between 18.00 and 6.00, however this was not possible due to time and manpower constraints. In all months except August, data from two consecutive weeks were combined at each site for the construction of flower-visitor webs.

The number of floral units observed was not stipulated since floral density varied between species and within a species throughout the plots. The flowers observed were limited to those in an area of approximately $1m^3$ since this was considered the maximum area that could reliably be observed by a single person. Within this constraint, observed flowers were chosen at random as far as possible. Where possible, different sets of flowers of each species were watched during different observations, however for rare species it was often only possible to watch the same set of flowers. One visit was recorded every time a visitor made contact with the sexual parts of a floral unit, regardless of the purpose of the visit. If a visitor left and then returned to the same flower this was counted as a second visit.

To enable accurate identification of visitor species, an attempt was made to catch all insect visitors using either sweep nets or by transferring them directly to a vial. Some easily recognisable species such as honeybees (*Apis mellifera*) were not captured. If the number of floral units being observed was greater than one, observers waited before catching an insect to allow it to visit other flowers. When visitors were not caught, a description of size and colouration was recorded where possible. All flower visitors observed were insects in the orders Hymenoptera (bees, wasps or ants), Diptera (flies), Coleoptera (beetles), Lepidoptera (butterflies or moths) and Hemiptera (bugs).

Ideally each observation would have been randomly allocated within a three-hour time slot. Whilst some attempt to do this was made in that plant species were never observed in the same order, complete randomisation of the times at which species were observed was not feasible due to time limitations. In some weeks sampling times were also limited by weather conditions since observations were not conducted during rain, after heavy rain showers or in high winds. There was no minimum temperature requirement for observations since temperature varied throughout the day.

Climate readings (relative humidity and temperature) were recorded for each flower observation using a Vaisala HMI 31 humidity and temperature probe. This was placed in the shade approximately 1m above the ground in a tree close to the observed flowers.

### 6.2.3 Insect identification and classification

Captured insects were transferred to killing vials, pinned, and compared to a reference collection of identified insects caught in previous field seasons. All insects were subsequently identified to the highest taxonomic level possible by taxonomists (bees and flies), or using museum collections (wasps, beetles and bugs) (see Chapter 5 Section 5.2.3 for further details). Juvenile Hemiptera were grouped since these are difficult to identify to species. Butterflies were identified to species using Larsen (1991). Ant visitors were not identified beyond family and were grouped as

Formicidae spp. for analysis. It was more difficult to identify insects that were not caught. The order could be determined for all except one of the uncaptured visitors. However, for many taxa it was more difficult to identify beyond this.

Flower visitors were identified to one of four different levels: species, morphospecies, morphogroup or unknown. Species incorporated all visitors that could be accurately identified to species level. Morphospecies were defined as a group of species in the same genus that looked morphologically similar but could not be confirmed as a species. A large proportion of wasp and beetle visitors were assigned to morphospecies since taxonomic assistance was not available for the identification of these to species level. Morphogroups were defined as a collection of species from the same taxonomic family between which it was impossible to identify in the field. For example, all unidentified butterflies in the family Lycaenidae were grouped as Lycaenidae spp. Large bees in the genera *Amegilla* and *Anthophora* (Apidae, tribe Anthophorini), *Tetralonia* and *Tetraloniella* (Apidae, tribe Eucerini) are fast flying and can be difficult to catch so were grouped as large Apidae spp. Some visitors could not be assigned to morphogroups so these were grouped as unknown species within an order. Unidentified bee species were grouped into categories based on their size: medium bee spp. (c.1-2cm) or small bee spp. (smaller than 1cm). Where appropriate size information was not available, bees were grouped as unknown bee spp. The identification of insects to morphospecies has been used in previous food web and plant-pollinator web studies where species level identification was not possible (Memmott 1999).

All species, morphospecies, morphogroups and unknown groups are collectively referred to as 'visitor types'. Forty two per cent of flower visitors were identified to species, 17% were assigned to a morphospecies, 26% were assigned to a morphogroup, and 17% belonged to an unknown category within a particular order.

### 6.2.4 Construction of quantitative flower-visitor interaction webs

*(a) Seasonal interaction webs for each site*

Quantitative flower-visitor interaction webs were constructed for all data collected during two weeks of sampling in each month at each site. In each web, the visits to each plant species were weighted in proportion to the floral abundance of the species in the plot during that sampling week. This was done to account for different floral abundances between species, and plant species with larger numbers of flowers are explicitly assumed to have received more flower visits during the same 20 minute observation period.

An interaction frequency for each interaction between a visitor type and a plant species in each observation period was calculated as follows:

$$\text{interaction} = \frac{\text{number of visits}}{\text{number of floral units observed}} \times \begin{array}{c}\text{total floral units for plant}\\ \text{species in that week}\end{array}$$

For example, 5 *Apis mellifera* visits to 10 floral units of a plant species with an overall abundance of 100 floral units would be represented by an interaction frequency of 50 in the interaction web (calculated as (5/10) ×100).

Although weighting the data in this way is not as accurate as more intensive sampling of species with greater floral abundances, this gives some idea of the probable frequencies of interactions across plant species.

*(b) Webs for daily time periods within each seasonal web*

To examine the daily temporal patterns within each seasonal flower-visitor web, four additional interaction webs were constructed from each seasonal web using the data from each three-hour time period. Thus at each seasonal time an overall web and four webs, one for each time period, were constructed for each site.

All flower-visitor interaction webs were drawn by Dr Jane Memmott (University of Bristol) using software written in Mathematica (Wolfram Research).

### *(c) Descriptive web statistics*

Connectance and the linkage levels of plant and visitors were calculated for each seasonal web. Connectance is the fraction of realised links in the web and can be used to measure the generalisation level of the web. Connectance (C) is calculated as follows:

$$C = \frac{I}{V \times P}$$

Where I is the observed number of interaction types, V is the number of visitor types and P is the number of plant species.

Linkage levels denote the mean number of interaction types per plant species or visitor type and are a measure of generalisation. Species or visitor types with high linkage levels utilise many partners and are therefore more generalised than those with lower linkage levels. The linkage levels of plant species ($L_P$) and visitor types ($L_V$) in each seasonal web were calculated as follows:

$$L_P = \frac{I}{V} \qquad L_V = \frac{I}{P}$$

Measures of connectance and linkage levels should strictly only be calculated for webs in which all plants and visitors have been resolved to species. Since not all visitors in the seasonal webs could be identified to species, these statistics for these webs are potentially inaccurate since each unknown group could represent more than one species, or some of the visitors grouped as unknowns could be species already identified in the web and so be represented twice. The linkage level for visitors was also calculated for only visitors identified to species or morphospecies. Calculating connectance and plant linkage levels using only visitor species and morphospecies would not be appropriate as some observed visitors to plants would need to be ignored.

### 6.2.5 Comparison of flower-visitor interactions over daily time

For each seasonal web, a null model was used to compare the observed number of interaction types present in each time period to the number of interaction types per time period in a series of randomly constructed webs. An interaction type is defined as a connection between a specific plant species and visitor type; e.g. between plant species A and visitor type B.

*(a) Overall data*

For each seasonal web at each site, the calculated interaction frequencies used to construct the observed webs were randomised in the following way:

(i) All observed plant-visitor interaction types were maintained. No new combinations were made since there might have been biological reasons why particular interaction types could not have occurred.

(ii) Each interaction in the observed web was randomly assigned to one of the four time periods. E.g. if the interaction frequency between plant species A and visitor type B was 20, this interaction was randomly assigned to one of the four time periods 20 times so that the randomly generated overall web also had an interaction frequency of 20 for this interaction.

(iii) Each time period maintained its total interaction frequency, hence preserving the overall daily pattern.

(iv) Using this procedure, 1000 webs were generated using a computer program written using C++ by Dr Denis Roze (University of Edinburgh).

(v) The number of interaction types in each time period in the observed web was compared to the distribution of number of interaction types in the equivalent time period for the 1000 randomised webs. The interpretation of statistical significance is conservative in that I have used a two-tailed approach, i.e. I regard a difference between the observed value and the randomly generated values as significant if the observed fell in or below the bottom 2.5% or in or above the top 97.5% of the randomly generated distribution of values.

*(b) By visitor group*

The number of interaction types for each time period in the observed webs and the randomly assembled webs were also compared for each visitor group. Visitors were assigned to the following groups: bees (Hymenoptera), wasps (Hymenoptera), ants (Hymenoptera), flies (Diptera), beetles (Coleoptera), bugs (Hemiptera), and butterflies and moths (Lepidoptera). Each visitor group incorporated visitors from a single insect order, although the Hymenoptera were divided into bees, wasps and ants.

### 6.2.6 Patterns of shared visitors through daily time

*(a) For all plant species*

If plant species at Mpala partition shared pollinators in daily time, shared pollinators should visit different plant species at different times of day. Pollinators were not identified in this study therefore this prediction was examined for shared flower visitors. Visitor species (including identified species and morphospecies) visiting multiple plant species were identified for each seasonal web. The plant species visited by these visitor species were compared between time periods to identify whether:

(i) Shared visitor species visited different plant species in different time periods

(ii) Shared visitor species visited multiple plant species in a single time period

Plant species sharing visitors across time periods could be partitioning the visitors in daily time whereas plant species sharing visitors in a single time period could be competing for visits.

*(b) For acacia species*

The above information was used to examine whether acacias shared visitors with other plant species in the community, and how visits from shared visitor species were structured in daily time. *Senegalia brevispica* was sampled in all seasonal webs at both sites, *V. gerrardii* was sampled in the May web at Turkana Boma, *V. nilotica* was sampled in the June and July webs at Turkana Boma and *V. etbaica* was sampled in the August web at Turkana Boma.

### 6.2.7 Daily climate variation

Variation in the composition and diversity of visitors and interactions in daily time could be due to climatic variation throughout the day. Temperature and relative humidity were recorded half-hourly at fixed locations during full day visitation sampling of acacia species (Chapter 5). Several of these days coincided with web sampling at Turkana Boma in June, July and August 2004. Data collected on 21st June, 22nd June, 16th July, 21st July, 18th August and 20th August 2004 were used to compare the differences in relative humidity and temperature across the twelve-hour web sampling day. These data, rather than those recorded during flower observations for webs, were used since they were taken from a fixed point and were recorded at regular time intervals throughout entire days.

## 6.3 Results

### 6.3.1. To what extent do visitors, plants and their interactions change across seasonal times, and are these patterns consistent across sites?

*(a) Flowering plants*

During the study I recorded a total of 95 flowering plant species belonging to 29 families, with 70 species recorded at Turkana Boma and 54 at Junction. Twenty nine species flowered at both sites. Some examples of these are shown in Figs. 2.11 and 2.12. The diversity of flowering plant species varied across months at both sites with more species in the May, June and August webs and far fewer species in July (Table 6.1). High diversities followed high levels of rainfall (see Table 2.1); i.e. rainfall was high in April, May and July, but lowest in June, which preceded the July web. The flowering plant species that were present in each seasonal web at each site are listed in Appendix 7, along with the number of floral units recorded in each sampling week.

The composition of the flowering plant species communities also varied between months at both sites, although at Turkana Boma eight species flowered in all seasonal webs and at Junction 11 species flowered in both webs (Appendix 7). Four species flowered in all seasonal webs at both sites: *Monechma* sp. B (Acanthaceae), *Ipomoea sinensis* (Convolvulaceae), *Senegalia brevispica* (Fabaceae) and *Pavonia* *gallaensis* (Malvaceae). Whilst a large number of species flowered in response to rainfall, *Barleria spinisepala* (Acanthaceae) flowered when it was drier, and formed a large proportion of the total floral abundances at both sites in July.

### *(b) Insect visitors*

In total, 174 visitor types were recorded (see Appendix 8). Of these, 82 were distinct species and 54 were morphospecies (Table 6.2). The remaining visitors were grouped within one of 26 morphogroups or 12 unknown categories within an order. I observed 140 visitor types at Turkana Boma and 75 at Junction. Almost all flower visitors belonged to one of four insect orders: Hymenoptera (bees, wasps and ants), Diptera (flies), Coleoptera (beetles) or Lepidoptera (butterflies and moths). I recorded only 4 visits by Hemiptera (bugs). Bee, wasp and fly visitors were recorded in all seasonal webs. Ant and lepidopteran visitors occurred in five webs, and beetle visitors in four webs. Bugs were recorded in three webs.

The number of bee visitor types (70) was more than twice the number of visitor types recorded for any other visitor group. I recorded 27 visitor types for wasps, 31 for flies, 28 for beetles and 15 for butterflies and moths. The number of species, morphospecies, morphogroups and unknown groups identified for each visitor group are shown in Table 6.2.

Table 6.1 Number of visitor types, flowering plant species, observed flowering plant species (for which visitation was quantified), total floral units, total hours of observation, number of interaction types, total flower visits and total interaction frequency for each flower-visitor web.

| | Visitor types | Total flowering plant species | Plant species observed | Total floral units | Hours of observation | Number of interaction types | Total flower visits | Total interaction frequency |
|---|---|---|---|---|---|---|---|---|
| **Turkana Boma** | | | | | | | | |
| May | 84 | 54 | 38 | 83621 | 71.33 | 160 | 833 | 61633 |
| June | 66 | 42 | 32 | 9475 | 65.00 | 105 | 395 | 11797 |
| July | 16 | 14 | 10 | 1814 | 16.00 | 22 | 54 | 3069 |
| August | 26 | 48 | 31 | 34224 | 33.67 | 46 | 366 | 2211 |
| **Junction** | | | | | | | | |
| June | 63 | 51 | 35 | 28082 | 72.33 | 99 | 678 | 19176 |
| July | 22 | 14 | 12 | 1281 | 22.33 | 26 | 66 | 309 |

Table 6.2 Total numbers of species, morphospecies, morphogroups and unknown groups for each visitor group across all seasonal webs at both sites

| | Hymenoptera | | | Diptera | Coleoptera | Lepidoptera | Hemiptera | Total |
|---|---|---|---|---|---|---|---|---|
| | bee | wasp | ant | | | | | |
| species | 52 | 0 | 0 | 15 | 5 | 10 | 0 | 82 |
| morphospecies | 6 | 23 | 0 | 4 | 20 | 1 | 0 | 54 |
| morphogroup | 6 | 3 | 1 | 10 | 2 | 4 | 0 | 26 |
| unknown group | 6 | 1 | 0 | 2 | 1 | 0 | 2 | 12 |
| **Total** | **70** | **27** | **1** | **31** | **28** | **15** | **2** | **174** |

### *(i) Comparisons between seasonal webs at each site*

The number of visitor types observed varied between months at both sites, with higher diversities in months with higher flowering plant species diversities (Table 6.1, Fig. 6.1). Higher diversities were recorded during months in which more plant species were observed (Pearson's correlation: r=0.840, p=0.036) and this correlation may in part be a sampling artefact of a greater number of observations when more plant species are present. Appendix 8 details all visitor types recorded in each web and the level to which they could be identified. The identities of flower visitors also varied between months at each site. At Turkana Boma, 38 visitor types (14 species, 6 morphospecies, 12 morphogroups and 6 unknown groups) were recorded in more than one seasonal web. *Apis mellifera* was observed in all four webs. Five species, all bees, were observed in three of the four webs at Turkana Boma: *Ceratina nyassensis* (Apidae), *Plebeina hildebranti* (Apidae), *Lipotriches* (*Lipotriches*) sp. 1 (Halictidae), *Pseudapis* (*Pseudapis*) sp. 1 (Halictidae) and *Megachile* (*Chalicodoma*) sp. 2 (Megachilidae).

At Junction, 10 visitor types (4 species, 1 morphospecies, 1 morphogroup and 4 unknown groups) were recorded in both webs (Appendix 8). Three bee species and one butterfly were recorded in both webs: *Amegilla penicula* (Apidae), *Halictus* (*Seladonia*) sp. 1 (Halictidae), *Pseudapis* (*Pseudapis*) sp. 1 (Halictidae) and *Eurema brigitta brigitta* (Pieridae).

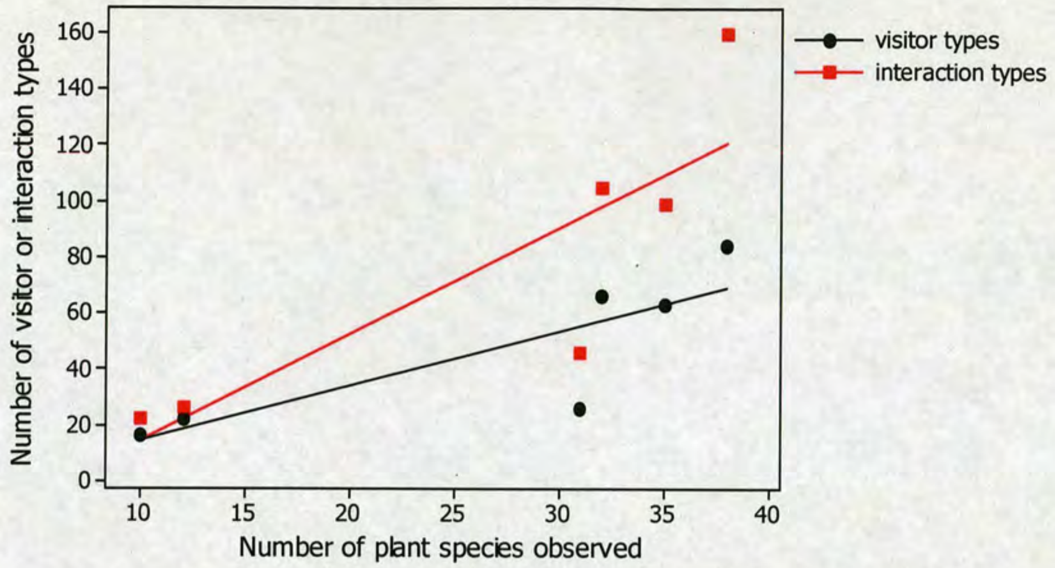


Figure 6.1 The relationship between the number of plant species observed and the number of visitor types and interaction types. Each datapoint represents a seasonal web. Regression lines are shown for each data set.

*(ii) Comparisons between sites*

The diversity of visitor types was similar at both sites in June and July (Table 6.1). Overall, 41 visitor types were observed at both Turkana Boma and Junction (Appendix 8). These incorporated 17 species, 5 morphospecies, 13 morphogroups and 6 unknown categories. In June, five bee species were observed at both sites: *Amegilla calens* (Apidae), *Apis mellifera* (Apidae), *Halictus* (*Seladonia*) sp. 1 (Halictidae), *Lipotriches* (*Lipotriches*) sp. H (Halictidae) and *Patellapis* sp. A (Halictidae). One beetle, *Megalognatha meruensis* (Chrysomelidae), and one butterfly, *Freyeria trochylus trochylus* (Lycaenidae), were also observed at both sites in June. Only one species, the bee *Ceratina nyassensis* (Apidae) was observed at both sites in July.

*(c) Flower-visitor interactions*

Overall, 2392 flower visits were observed at both sites (1648 at Turkana Boma and 744 at Junction) and 411 interaction types were recorded (313 at Turkana Boma and 122 at Junction). Twenty interaction types were recorded in both sites. Details of the interaction types present in each seasonal web are given in Appendix 9. The numbers of flower visits and interaction types were greater in months with higher flowering plant species diversity (Table 6.1, Fig. 6.1). There were significant correlations between the number of plant species observed and number of flower visits (r=0.925, p=0.008) and number of plant species observed and number of interaction types (r=0.850, p=0.032). Again, these correlations may be an artefact of sampling effort.

The flower-visitor interaction webs for each sampling month at each site are shown in Figures 6.4-6.6. Bees were dominant visitors in all webs with the greatest diversities of visitor types and interaction types (see Appendix 10). Bees accounted for 38- 56% of total visitor types, 36-60% of interaction types and 30-65% of total visits in each seasonal web. Wasps and flies were also responsible for large numbers of visits and interaction types. Wasps formed 7-27% of visitor types, 5-27% of interaction types and 3-35% of visits. Flies formed 8-21% of visitor types, 7-18% of interaction types and 4-14% of visits.

The connectance values represent the proportion of realised links in the web and give a measure of generalisation for the entire web. Connectance values were higher for the seasonal webs with fewer plant species and visitor types (Table 6.3). Linkage levels show the mean number of interacting partners for plant species, visitor types and visitor species (species and morphospecies) in each seasonal web and are a measure of the generalisation levels for each group (Table 6.3). Linkage levels were generally lower in the July webs at both sites, which had the lowest diversities of plant species and visitor types. However, the linkage level for plant species at Turkana Boma in August was even lower than that for the July web, despite the visitor linkage levels being equivalent to those in May and June (Table 6.3). Several plant species in this web received no visits which resulted in the lower overall linkage level for plants.

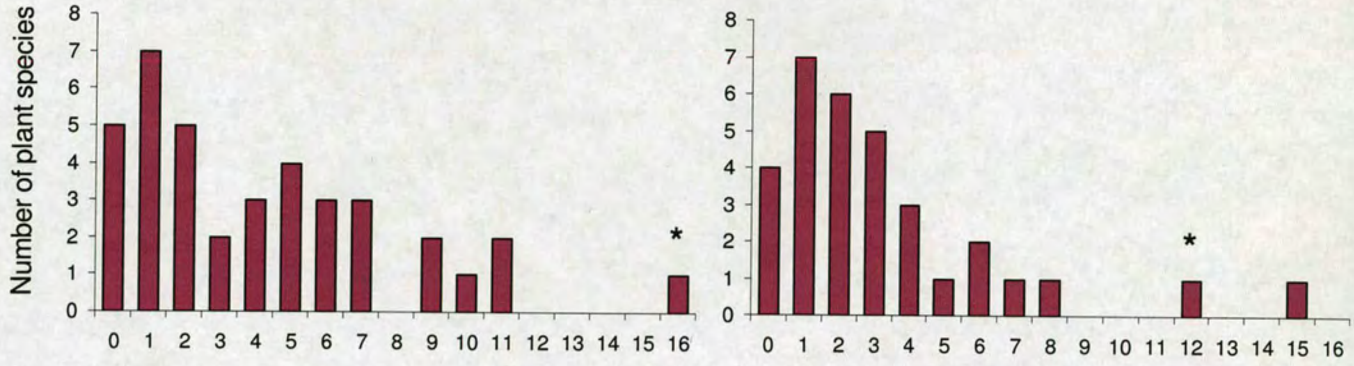
Plant species received visits from up to 16 visitor types (Fig. 6.2). *Senegalia brevispica* was visited by the most visitor types in three webs (16 in May, 8 in July and 5 in August at Turkana Boma, 8 in July at Junction) and by large numbers of visitor types in other seasonal webs (Fig. 6.2). Other plant species with high diversities of visitor types were *Gutenbergia cordifolia* (Asteraceae; 11 in May and 15 in June at Turkana Boma, 9 in June at Junction) and *Monechma* sp. B (Acanthaceae; 6 at Turkana Boma in June and 12 at Junction in June).

Visitor types were found on up to 11 plants, although visitors identified to species or morphospecies were only found on up to 5 plants (Fig. 6.3). Ants (Family

Formicidae) visited the most plant species in several webs, however this visitor group could include several species and is therefore not comparable to species or morphospecies. Visitor species or morphospecies found on a large number of plant species included *Apis mellifera* (4 plant species in May, 3 in June and 5 in August at Turkana Boma, 5 in June at Junction), *Halictus* (*Seladonia*) sp. C (Halictidae) (4 in June at Turkana Boma), *Ceratina nyassensis* (Apidae) (3 in July at Turkana Boma) and *Plebeina hildebranti* (Apidae) (4 in August at Turkana Boma). The beetle *Coryna ?apicornis* (Meloidae) was found on 4 plant species in the June web at Turkana Boma.

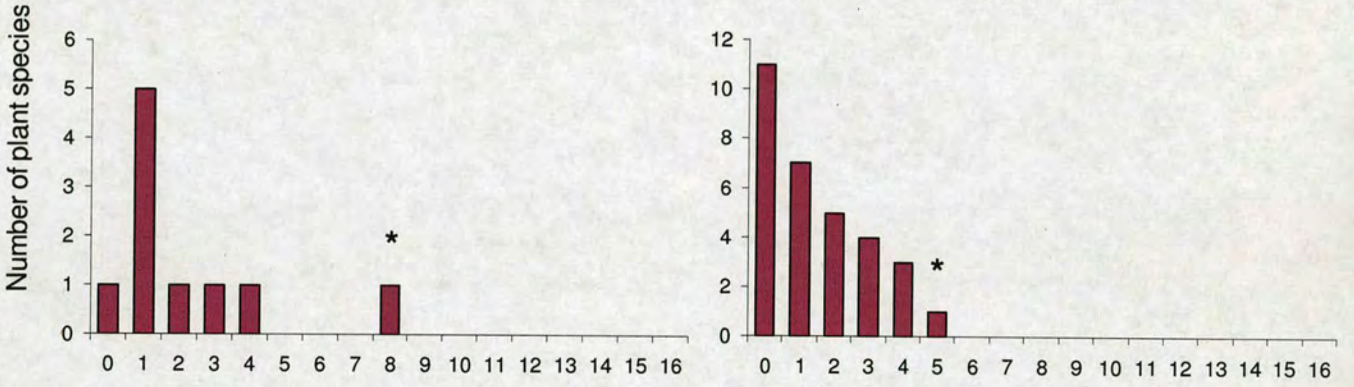
Table 6.3 Connectance and linkage levels of plant species, visitor types and visitor species (including morphospecies) for each seasonal web. See methods for calculations. Since linkage levels represent the mean number of interaction types for each group the standard error is also shown.

| | **Linkage levels for** | | | |
|---|---|---|---|---|
| | **Plant species** | **Visitor types** | **Visitor species** | **Connectance** |
| **Turkana Boma** | | | | |
| May | 4.21 ±0.62 | 1.90 ±0.20 | 1.57 ±0.11 | 0.050 |
| June | 3.28 ±0.60 | 1.59 ±0.16 | 1.35 ±0.11 | 0.050 |
| July | 2.20 ±0.74 | 1.38 ±0.18 | 1.20 ±0.20 | 0.138 |
| August | 1.48 ±0.27 | 1.77 ±0.35 | 1.56 ±0.28 | 0.057 |
| **Junction** | | | | |
| June | 2.91 ±0.52 | 1.57 ±0.16 | 1.36 ±0.12 | 0.045 |
| July | 2.17 ±0.69 | 1.18 ±0.11 | 1.08 ±0.08 | 0.098 |



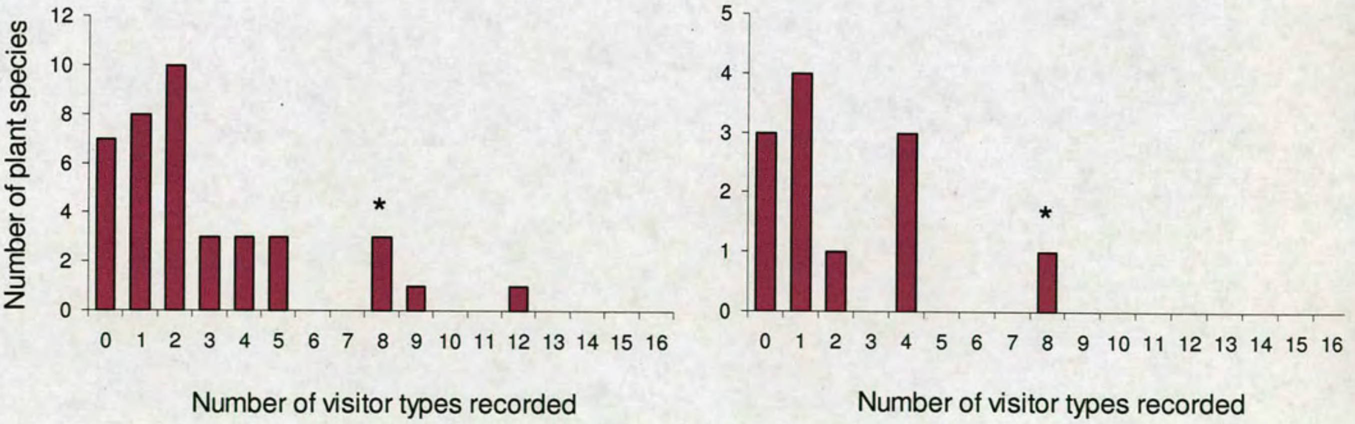
(a) Turkana Boma, May

(b) Turkana Boma, June



(c) Turkana Boma, July

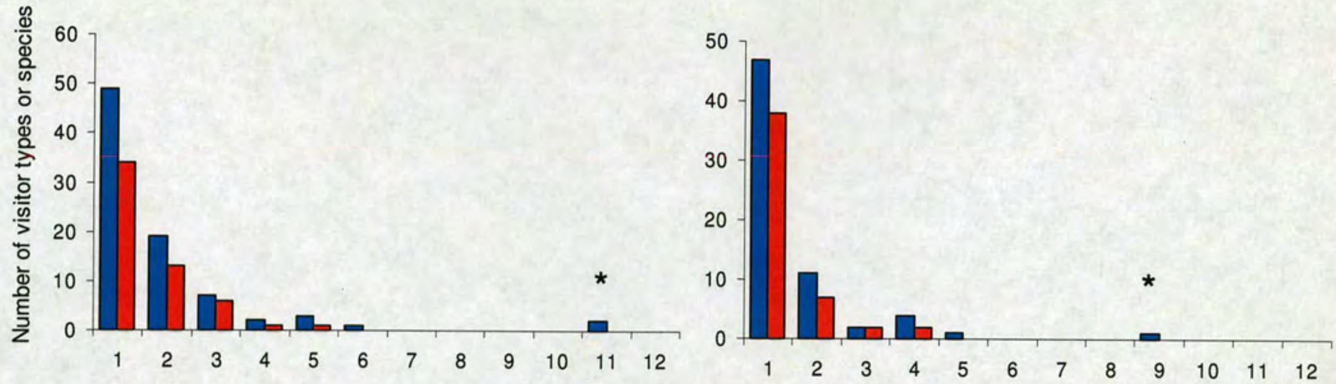
(d) Turkana Boma, August



(e) Junction, June

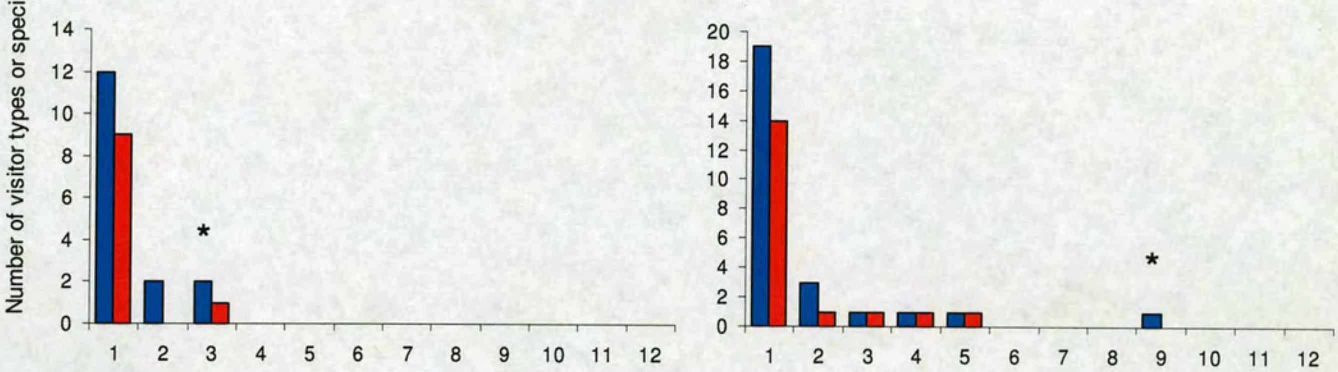
(f) Junction, July

Figure 6.2 Distribution of numbers of visitor types per plant species in each seasonal web. Asterices indicate the position of *S. brevispica* in each graph.



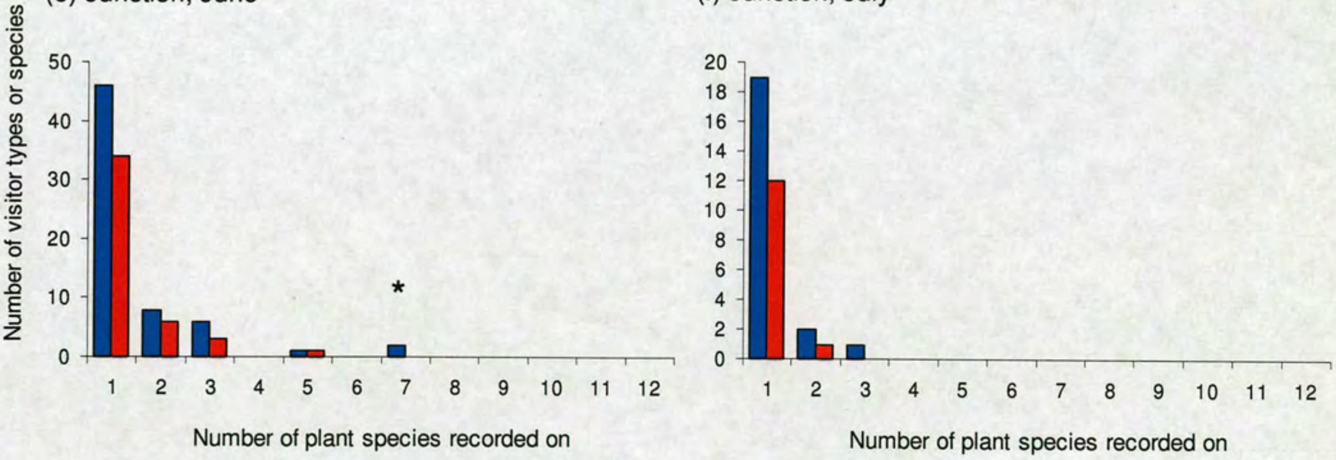
(a) Turkana Boma, May

(b) Turkana Boma, June



(c) Turkana Boma, July

(d) Turkana Boma, August



(e) Junction, June

(f) Junction, July

Figure 6.3 Distribution of numbers of plant species per visitor type (blue) and numbers of plant species per visitor species or morphospecies (red) in each seasonal web. Asterices indicate the position of ants (family Formicidae) on each graph.

In general, plant species present in multiple webs were visited by different visitors in different webs. For example, *Monechma* sp. B (Acanthaceae), which flowered in all seasonal webs at both sites, was visited by 9 bee species, 8 at Junction and 2 at Turkana Boma. Only *Apis mellifera* visited flowers of this species in both sites. Six of the bee species observed at Junction visited other flowering plant species at Turkana Boma, although not *Monechma* sp. B. Furthermore, although *Apis mellifera* was active in all seasonal webs at Turkana Boma, it only visited *Monechma* sp. B flowers in the June web.

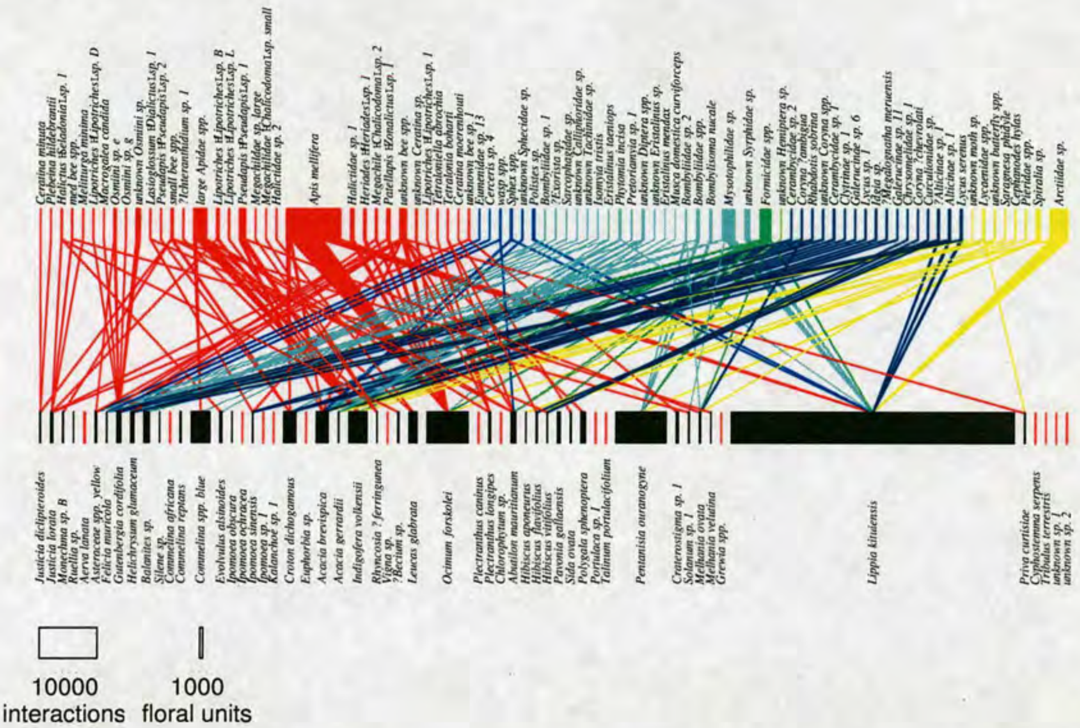
Only 13 interaction types involving visitor species or morphospecies were replicated across seasonal webs or across sites (Table 6.4). These visitors were bees, wasps and a chrysomelid beetle. At Turkana Boma, 6 interaction types were repeated across seasonal webs, all of which involved bees. At Junction the only interaction type found in both webs was between Eumenidae sp. 9 and *Monechma* sp. B. Three interactions were found at both sites in the same seasonal web, whilst 3 were found at both sites in different seasonal webs.

Curiously, although *Barleria spinisepala* had the greatest floral abundance at in the July web at Junction, no visitors were observed (Fig. 6.6). This species was visited in the June, July and August webs at Turkana Boma and the June web at Junction.

Table 6.4 Interaction types replicated across seasonal webs. TB: Turkana Boma, J: Junction.

| Family | Visitor species | Plant species | Webs |
|---|---|---|---|
| **bees** | | | |
| Apidae | *Apis mellifera* | *Senegalia brevispica* | May & August, TB |
| Apidae | *Apis mellifera* | *Leucas glabrata* | June J, August TB |
| Apidae | *Apis mellifera* | *Lippia kituiensis* | May & June, TB |
| Apidae | *Xylocopa somalica* | *Leucas glabrata* | June J, August TB |
| Halictidae | *Pseudapis* (*Pseudapis*) sp. 1 | *Senegalia brevispica* | May & August, TB, July J |
| Megachilidae | *Megachile* (*Chalicodoma*) sp. 2 | *Gutenbergia cordifolia* | May & June, TB |
| Megachilidae | *Megachile* (*Chalicodoma*) sp. 2 | *Monechma* sp. B | June & August, TB |
| Megachilidae | Osmiini sp. e | *Gutenbergia cordifolia* | May TB, June J |
| Megachilidae | *Heriades* (*Heriades*) sp. 1 | *Ocimum forskolei* | May & June, TB, June J |
| Megachilidae | *Heriades* (*Heriades*) sp. 1 | *Plectranthus caninus* | June TB, June J |
| **wasps** | | | |
| Eumenidae | Eumenidae sp. 8 | *Helichrysum glumaceum* | June TB, June J |
| Eumenidae | Eumenidae sp. 9 | *Monechma* sp. B | June & July, J |
| **beetles** | | | |
| Chrysomelidae | *Megalognatha meruensis* | *Senegalia brevispica* | June TB, June J |

(a) Turkana Boma, May



(b) Turkana Boma, June

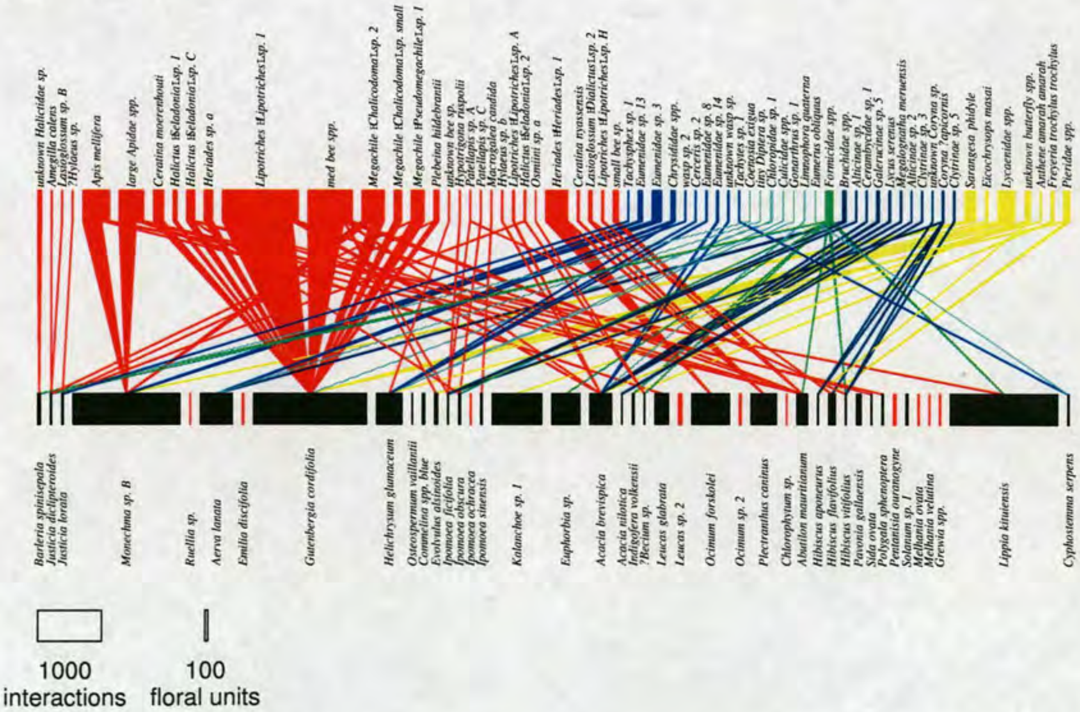
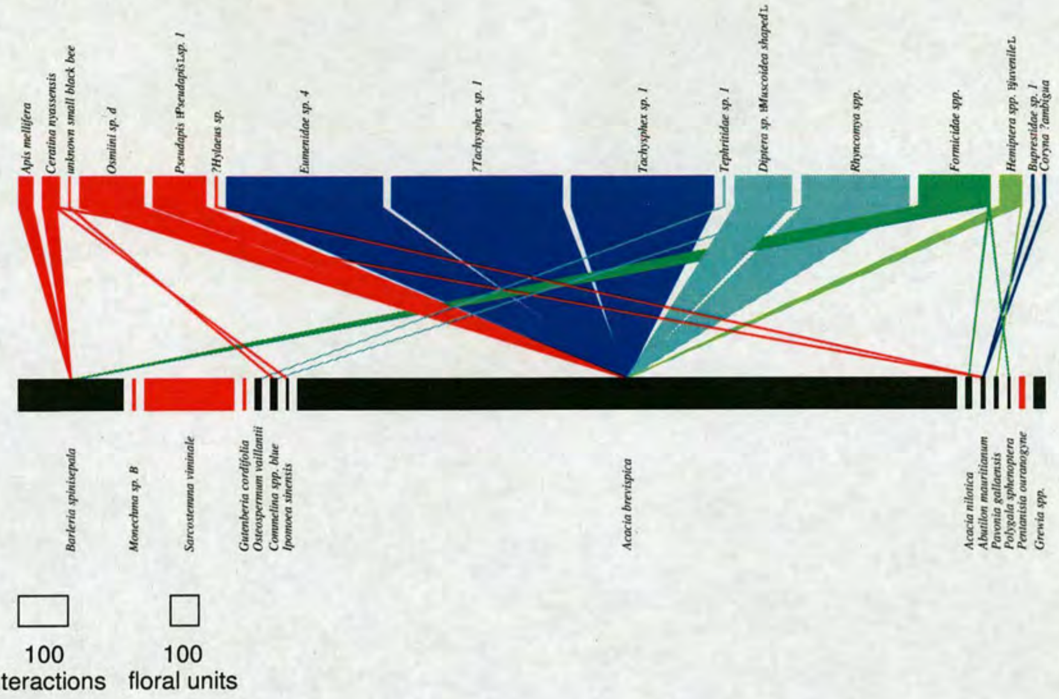


Figure 6.4 Flower-visitor interaction webs for Turkana Boma in (a) May and (b) June 2004. Floral unit abundance is represented by the width of the bars on the bottom line, with observed species coloured black and species that weren't coloured red. The relative frequency of visits by each visitor taxon is represented by a coloured bar on the top line; (from left to right) red: bees, medium blue: wasps, light blue: flies, green: ants, dark blue: beetles, yellow: butterflies and moths. The widths of the coloured lines connecting plants and visitors show the relative interaction frequency between them. Note that acacia species are referred to using old taxonomic names in this figure.

(a) Turkana Boma, July



(b) Turkana Boma, August

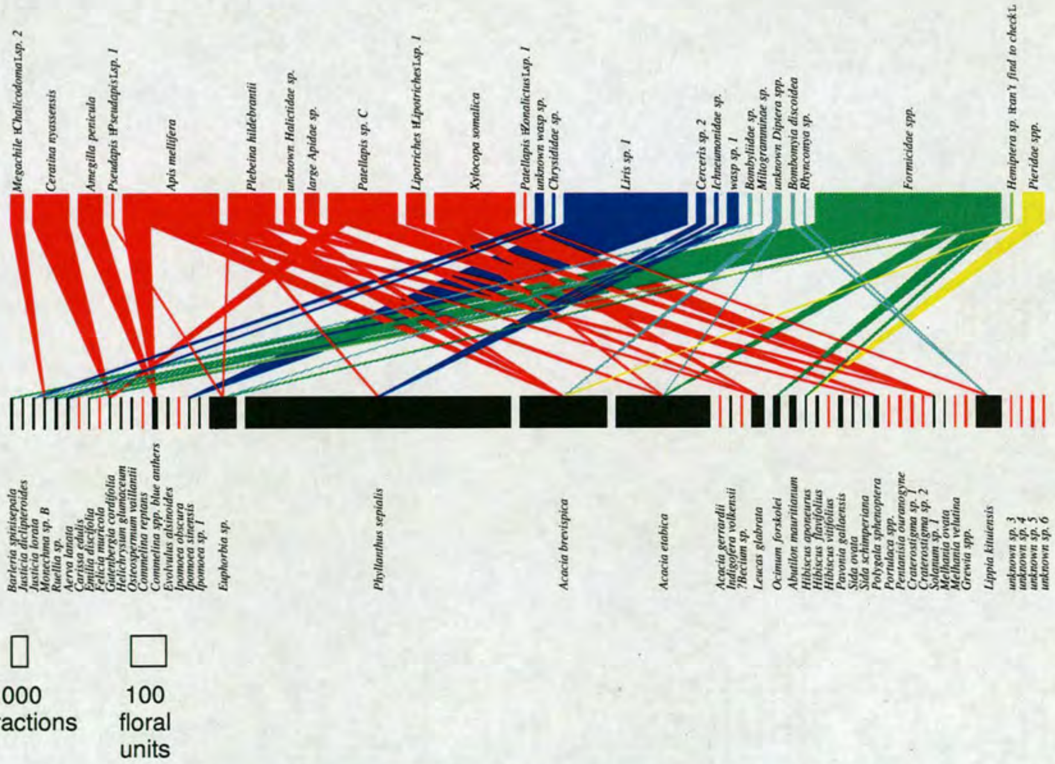
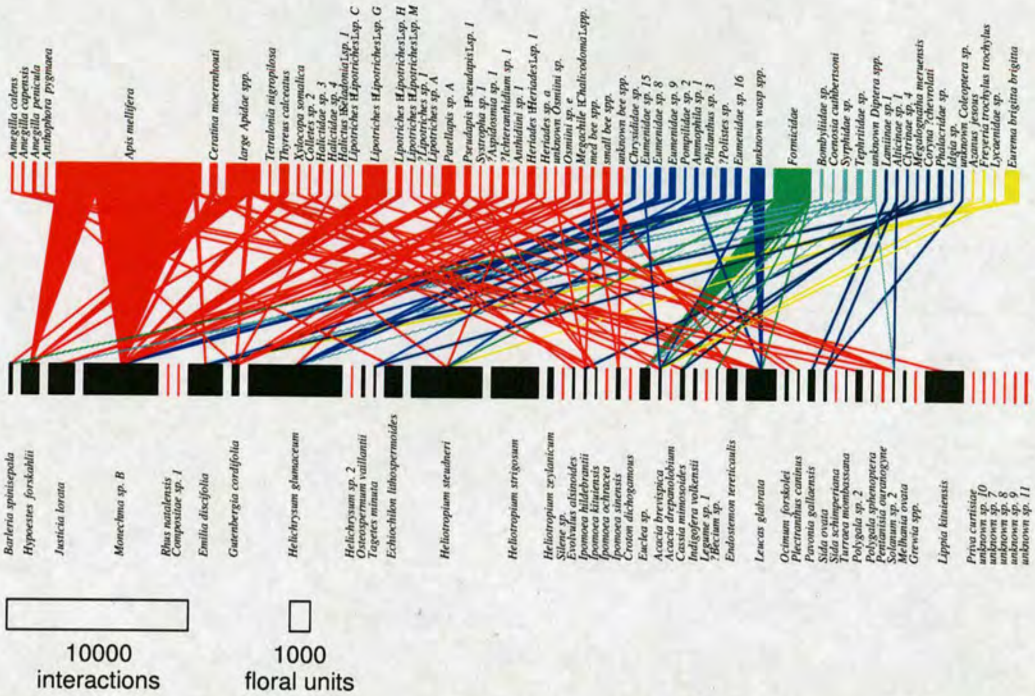


Figure 6.5 Flower-visitor interaction webs for Turkana Boma in (a) July and (b) August 2004. Floral unit abundance is represented by the width of the bars on the bottom line, with observed species coloured black and species that weren't coloured red. The relative frequency of visits by each visitor taxon is represented by a coloured bar on the top line; (from left to right) red: bees, medium blue: wasps, light blue: flies, green: ants, dark blue: beetles, yellow: butterflies and moths. The widths of the coloured lines connecting plants and visitors show the relative interaction frequency between them. Note that acacia species are referred to using old taxonomic names in this figure.

(a) Junction, June



(b) Junction, July

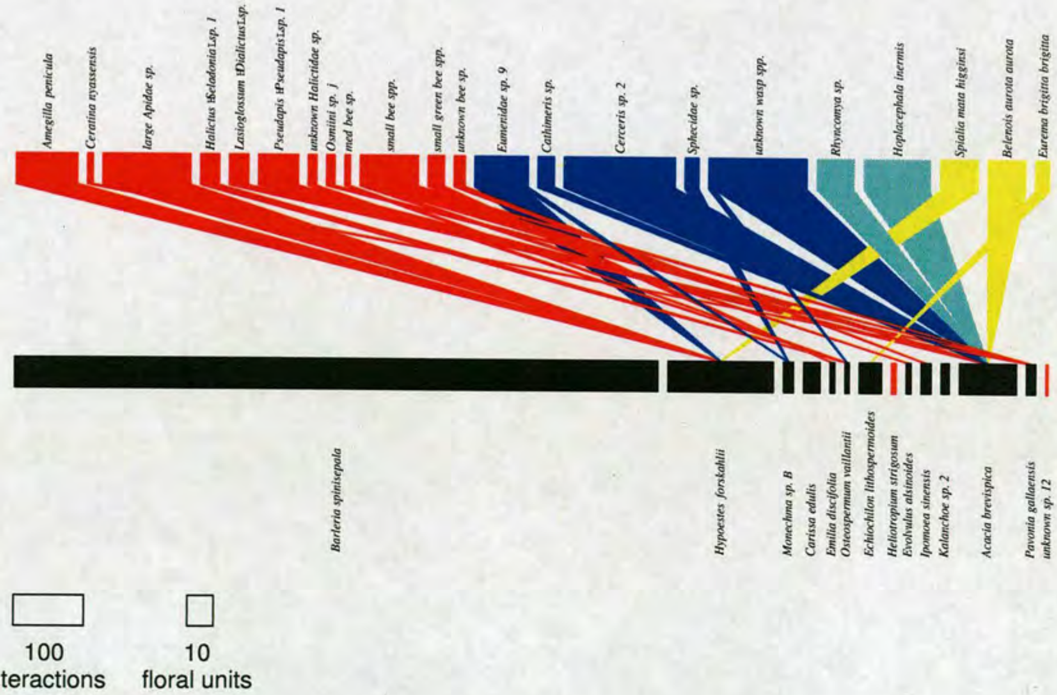


Figure 6.6 Flower-visitor interaction webs for Junction in (a) June and (b) July 2004. Floral unit abundance is represented by the width of the bars on the bottom line, with observed species coloured black and species that weren't coloured red. The relative frequency of visits by each visitor taxon is represented by a coloured bar on the top line; (from left to right) red: bees, medium blue: wasps, light blue: flies, green: ants, dark blue: beetles, yellow: butterflies and moths. The widths of the coloured lines connecting plants and visitors show the relative interaction frequency between them. Note that acacia species are referred to using old taxonomic names in this figure.

### 6.3.2 Within a seasonal web, to what extent are interactions structured in daily time?

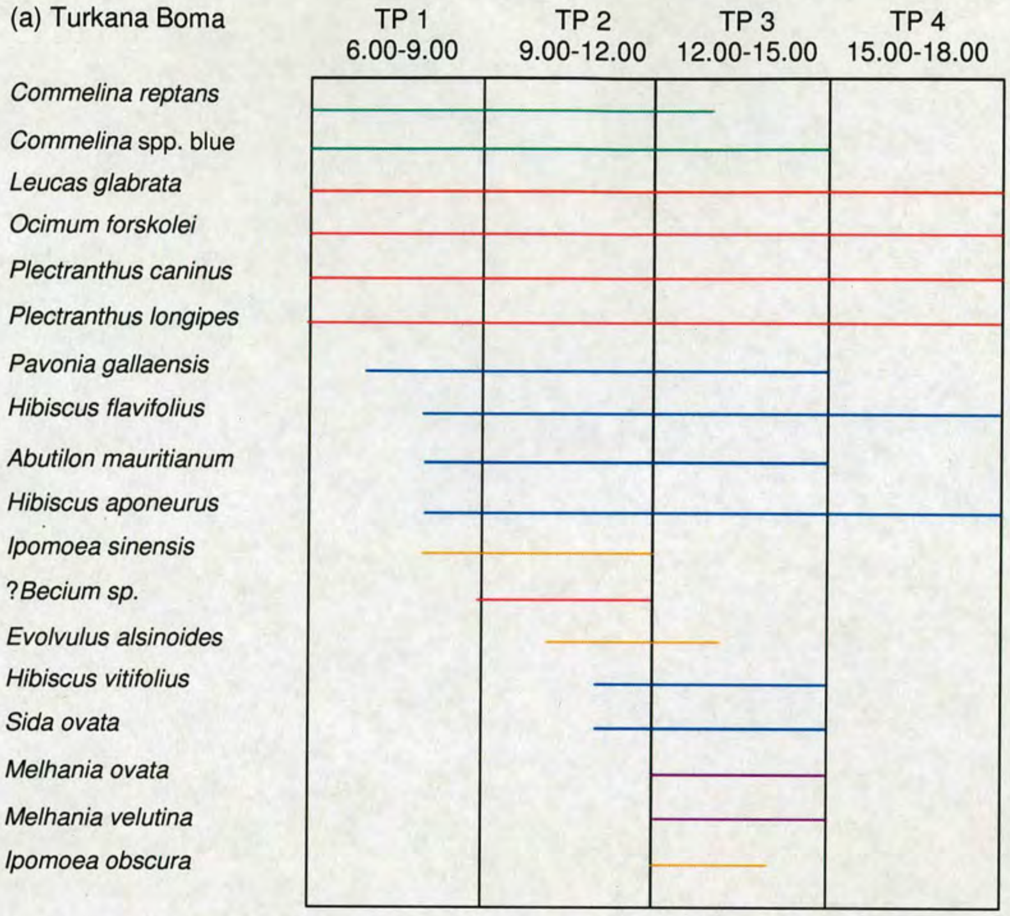
*(a) Bottom-up influences imposed by times of flower opening*

The flowers of some species were open throughout the sampling day, whereas the flowers of other species were open only for a part of each sampled day. Figure 6.7 shows the approximate times for which flowers were open for a selection of common plant species in the May and June webs at Turkana Boma, and in the June web at Junction. Since the availability of floral resources at both sites was structured in daily time, we might expect temporal structure to exist among flower-visitor interactions in these webs.

Flowers of species in the Malvaceae at Turkana Boma were open at different times during the day. For example, *Hibiscus flavifolius* and *H. aponeurus* were open from 8.00 until the end of the sampling day and were therefore open in all time periods. *Abutilon mauritianum* and *Pavonia gallaensis* opened at a similar time in the morning to these species, but their flowers were closed by 15.00 and therefore could not be observed in time period 4. *Hibiscus vitifolius* and *Sida ovata* were open between 11.00 and 15.00 and could only be observed in time periods 2 and 3.

Species with flower opening restricted mainly to time period 2 at Turkana Boma were *Ipomoea sinensis* (Convolvulaceae) and ?*Becium* sp. (Lamiaceae). Species with flower opening restricted mainly to time period 3 at the same site were *Melhania ovata* (Sterculiaceae), *M. velutina* (Sterculiaceae) and *Ipomoea obscura* (Convolvulaceae). *Evolvulus alsinoides* (Convolvulaceae) was open for part of time period 2 and part of time period 3.

Species with flower opening restricted mainly to time period 2 at Junction were *Ipomoea hildebrantii* (Convolvulaceae), *I. sinensis* (Convolvulaceae) and *Pavonia gallaensis* (Malvaceae). Species with flower opening restricted mainly to time period 3 at the same site were *Endostemon tereticaulis* (Lamiaceae) and ?*Becium* sp. (Lamiaceae). As at Turkana Boma, *Evolvulus alsinoides* (Convolvulaceae) flowered during part of time period 2 and time period 3.


(a) Turkana Boma

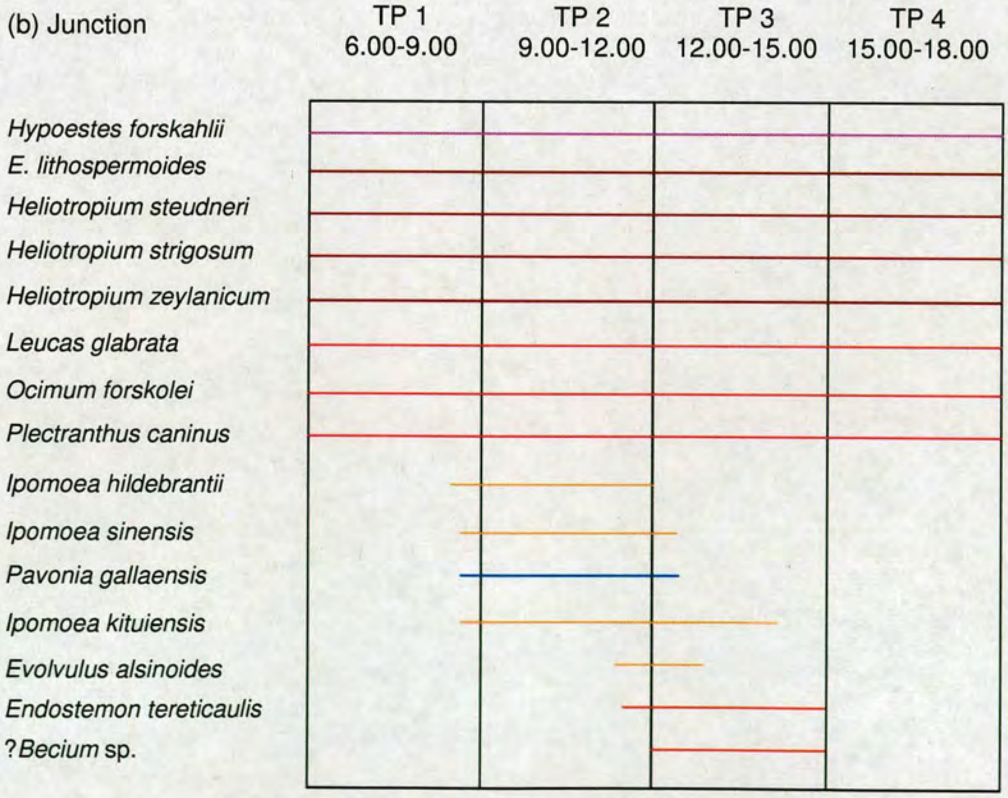

(b) Junction

Figure 6.7 Approximate flower opening times for common flowering plant species at (a) Turkana Boma in the May and June webs and (b) Junction in the June web. The different coloured lines represent different plant families: red: Lamiaceae, blue: Malvaceae, orange: Convolvulaceae, green: Commelinaceae, purple: Sterculiaceae, pink: Acanthaceae, brown: Boraginaceae.

*(b) Insect visitors*

In all seasonal webs the highest diversities of visitor types occurred in time periods 2 and 3 (Appendix 10). The lowest diversities of visitor types were recorded in time period 1. The only visitors active before 8.00 at Turkana Boma were flies, with fly, ant and bee visitors active between 8.00 and 9.00. At Junction no flower visits were observed before 8.00. Visitor types observed between 8.00 and 9.00 were bees (mostly large apid bees in the genera *Amegilla*, *Anthophora*, *Tetralonia* and *Tetraloniella*), flies or ants. The majority of visitors observed in time period 4 were observed between 15.00 and 16.00 and none were observed after 16.40. Since bees were the most frequent visitor group, these are considered in more detail than other visitor groups.

**Bees:** Bees were active in all time periods (Appendix 10). Bee diversity and numbers of bee visits were greatest during time periods 2 or 3 in all seasonal webs. All identified bee species were observed in either time period 2 or 3 in at least one of the seasonal webs (Appendix 9). No bees were observed in time period 1 in three webs (June and July at Turkana Boma and July at Junction) and bee species diversity in this time period was low; I only recorded the halictid bees *Lasioglossum* (*Dialictus*) sp. 1 and *Patellapis* sp. A, along with *Amegilla calens* (Apidae) and a small number of unidentified species of large apid bee in the genera *Amegilla*, *Anthophora*, *Tetralonia* or *Tetraloniella*. A greater number of bee species was observed in time period 4. These included three halictid bee species (*Lipotriches* (*Lipotriches*) sp. 1, *Lasioglossum* sp. B and *Halictus* (*Seladonia*) sp. C), five megachilid species (*Megachile* (*Chalicodoma*) sp. 2, *Megachile* (*Pseudomegachile*) sp. 1, *Heriades* (*Heriades*) sp. 1, *Heriades* sp. a and ?*Aspidosmia* sp.) and three apid species (*Apis mellifera*, *Ceratina moerenhouti* and *Xylocopa somalica*), along with a small number of unidentified large apid bees in the genera *Amegilla*, *Anthophora*, *Tetralonia* or *Tetraloniella*.

**Other visitors:** Wasps were active in time periods 2-4. The highest diversities of wasp visitors were observed in time period 3 in all webs. Ants were active in all time periods, although not in time period 1 in the June, July and August webs at Turkana Boma. Flies were active in all time periods with the highest diversities of visitors in either time period 2 or 3 in all webs. Beetles were active in all time periods, although only one beetle visitor was observed in time period 1 in the

May web at Turkana Boma. The highest diversities of beetle visitors were observed in either time period 2 or 3 in all webs. Butterflies and moths were active in time periods 2 to 4 although the time period with the highest diversity varied between seasonal webs (Appendix 10).

*(c) Flower-visitor interactions*

Flower-visitor interaction webs constructed for the 4 three-hour time periods in each seasonal web show the variation in numbers of interaction types, calculated interaction frequencies and visitor types active at different daily times (Figs. 6.8-6.13). The number of plant species observed, visitor types and interaction types for each time period in each seasonal web are shown in Tables 6.5 and 6.6. The flower-visitor interactions observed in each time period in each seasonal web are detailed in Appendix 9.

In all seasonal webs, the greatest numbers of interaction types were observed during time periods 2 or 3, with the fewest occurring in time period 1 (Appendix 10). Bees were responsible for the most interaction types in time periods 2 and 3 in all webs. Flies were responsible for the most interaction types in time period 1 in all webs except the June web at Junction, in which bees had the most interaction types. The visitor group with the most interaction types in time period 4 varied across webs.

The interactions occurring in each time period were restricted to plant species with open flowers. For example, *Evolvulus alsinoides* (Convolvulaceae) was open in time periods 2 and 3 in the May web at Turkana Boma and was visited only in time period 2 by flies and bees (Fig. 6.8). *Melhania ovata* (Sterculiaceae) was only open in time period 3 in the same web and was visited by bees. *Ipomoea sinensis* (Convolvulaceae) was open between 8.00 and 13.00 in the June web at Junction, and was observed in time periods 1-3 but only visited in time periods 2 and 3 by bees (Fig. 6.12).

The flowers of other plant species were open through the sampling day and observed in all time periods. Some plants were visited in all time periods, e.g. *S. brevispica* and *Balanites* sp. (Balanitaceae), which were both visited by a wide diversity of visitors in the May web at Turkana Boma (Fig. 6.8). *Leucas glabrata* (Lamiceae) was visited in all time periods in the June web at Junction and was visited by bees, wasps, butterflies and ants (Fig. 6.12). Other plant species were observed in all time periods but were only visited during some of these. For example, in the May web at Turkana Boma *Leucas glabrata* was visited by bees in time periods 1 and 2 but not visited in time periods 3 and 4 (Fig. 6.12).

### 6.3.3 Null modelling analysis of community-wide daily temporal structure

In all seasonal webs, the number of interaction types observed in each time period was significantly lower than those for the randomly assembled webs (Fig. 6.14). This is what we would expect to see if flower-visitor interactions were clustered in specific time periods. The number of bee interaction types observed in each time period was significantly lower than those in the randomly assembled webs in 22 time periods across six seasonal webs (Figs. 6.15-6.20). This suggests that most interactions involving bees were temporally structured.

Although there were significant differences in the number of interaction types between observed and randomised webs for all other visitor groups, there was no consistency across seasonal webs in the number of time periods for which significant differences were found for each group (Figs. 6.15-6.20). In general, time periods for which there were no significant differences involved relatively small numbers of interaction types.

After bees, wasps had the greatest number of time periods with significant differences between observed and randomised webs (21 time periods over 6 seasonal webs). The lowest level of temporal structure (excluding bugs which had a very low sample size) was observed for ants (9 time periods in 5 webs).

Table 6.5 Number of visitor types, flowering plant species with open flowers, observed flowering plant species, flower visits and interaction types per time period for each flower-visitor web at Turkana Boma. Interaction frequencies calculated for each time period are also shown.

| | **Visitor types** | **Plant species with open flowers** | **Plant species observed** | **Interaction types** | **Flower visits** | **Interaction frequency** |
|---|---|---|---|---|---|---|
| **May** | | | | | | |
| TS 1: 6.00-9.00 | 10 | 46 | 30 | 12 | 64 | 5400 |
| TS 2: 9.00-12.00 | 45 | 54 | 38 | 81 | 291 | 16959 |
| TS 3: 12.00-15.00 | 45 | 50 | 34 | 66 | 172 | 16561 |
| TS 4: 15.00-18.00 | 20 | 39 | 23 | 27 | 306 | 22713 |
| | **84** | **54** | **38** | **160** | **833** | **61633** |
| **June** | | | | | | |
| TS 1: 6.00-9.00 | 1 | 33 | 23 | 1 | 1 | 63 |
| TS 2: 9.00-12.00 | 38 | 41 | 31 | 53 | 133 | 4406 |
| TS 3: 12.00-15.00 | 37 | 42 | 32 | 55 | 206 | 4644 |
| TS 4: 15.00-18.00 | 17 | 33 | 23 | 18 | 55 | 2684 |
| | **66** | **42** | **32** | **105** | **395** | **11797** |
| **July** | | | | | | |
| TS 1: 6.00-9.00 | 1 | 10 | 6 | 1 | 4 | 371 |
| TS 2: 9.00-12.00 | 4 | 13 | 9 | 4 | 9 | 246 |
| TS 3: 12.00-15.00 | 13 | 13 | 9 | 16 | 39 | 2376 |
| TS 4: 15.00-18.00 | 2 | 10 | 6 | 2 | 2 | 74 |
| | **16** | **14** | **10** | **22** | **54** | **3069** |
| **August** | | | | | | |
| TS 1: 6.00-9.00 | 3 | 41 | 23 | 3 | 8 | 123 |
| TS 2: 9.00-12.00 | 13 | 47 | 30 | 20 | 112 | 722 |
| TS 3: 12.00-15.00 | 16 | 44 | 26 | 25 | 213 | 964 |
| TS 4: 15.00-18.00 | 4 | 38 | 21 | 10 | 33 | 402 |
| | **26** | **48** | **31** | **46** | **366** | **2211** |

Table 6.6 Number of visitor types, flowering plant species with open flowers, observed flowering plant species, flower visits and interaction types per time period for each flower-visitor web at Junction. Interaction frequencies calculated for each time period are also shown.

| | **Visitor types** | **Plant species with open flowers** | **Plant species observed** | **Interaction types** | **Flower visits** | **Interaction frequency** |
|---|---|---|---|---|---|---|
| **June** | | | | | | |
| TS 1: 6.00-9.00 | 5 | 46 | 29 | 5 | 55 | 480 |
| TS 2: 9.00-12.00 | 27 | 49 | 33 | 32 | 202 | 3703 |
| TS 3: 12.00-15.00 | 40 | 51 | 34 | 56 | 297 | 8986 |
| TS 4: 15.00-18.00 | 14 | 42 | 25 | 16 | 124 | 6007 |
| **Total** | **63** | **51** | **35** | **99** | **678** | **19176** |
| **July** | | | | | | |
| TS 1: 6.00-9.00 | 1 | 10 | 8 | 1 | 2 | 16 |
| TS 2: 9.00-12.00 | 11 | 14 | 12 | 12 | 32 | 132 |
| TS 3: 12.00-15.00 | 13 | 14 | 12 | 14 | 30 | 154 |
| TS 4: 15.00-18.00 | 2 | 11 | 9 | 2 | 2 | 7 |
| **Total** | **22** | **14** | **12** | **26** | **66** | **309** |

Turkana Boma, May

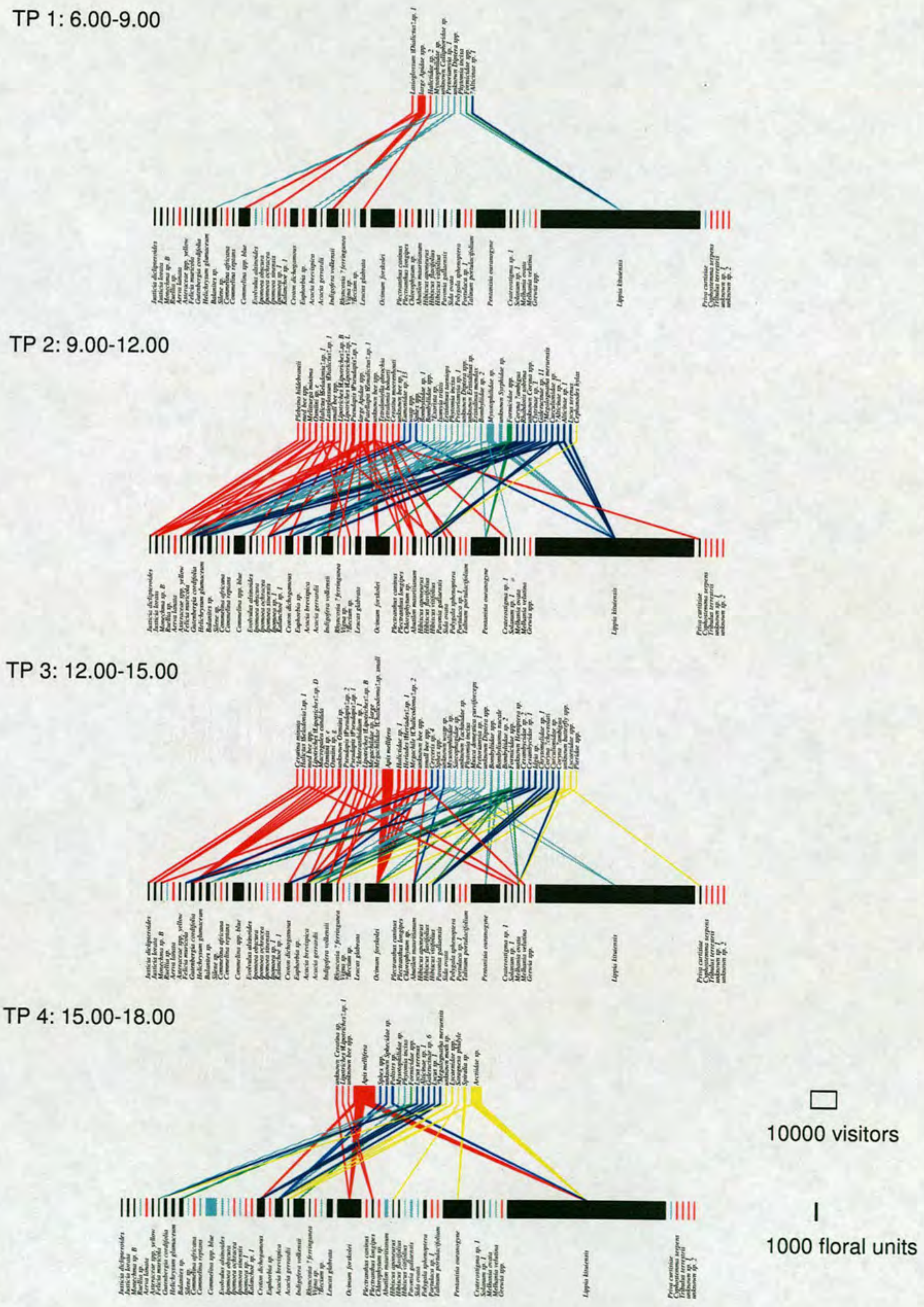
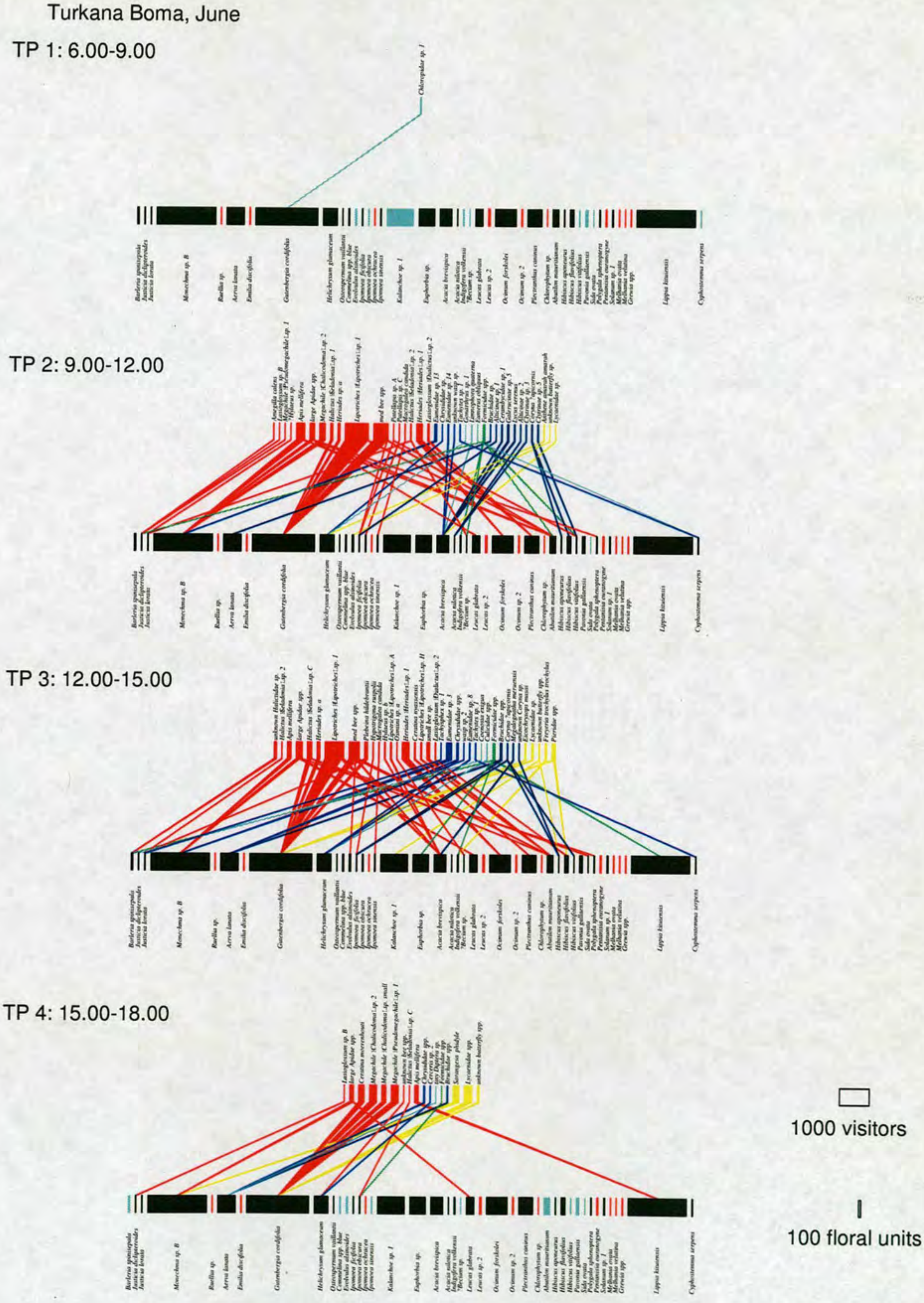


Figure 6.8 Flower-visitor interaction webs for each three hour time period at Turkana Boma in May. All webs are drawn to the same scale. Floral unit abundance is represented by the width of the bars on the bottom line, with observed species coloured black, unobserved species coloured red and species whose flowers were closed coloured blue. The relative frequency of visits by each visitor taxon is represented by a coloured bar on the top line. For further details refer to the legend for Figure 6.4.



Turkana Boma, June

TP 1: 6.00-9.00

TP 2: 9.00-12.00

TP 3: 12.00-15.00

TP 4: 15.00-18.00

Figure 6.9 Flower-visitor interaction webs for each three hour time period at Turkana Boma in June. All webs are drawn to the same scale. Floral unit abundance is represented by the width of the bars on the bottom line, with observed species coloured black, unobserved species coloured red and species whose flowers were closed coloured blue. The relative frequency of visits by each visitor taxon is represented by a coloured bar on the top line. For further details refer to the legend for Figure 6.4.

Turkana Boma, July

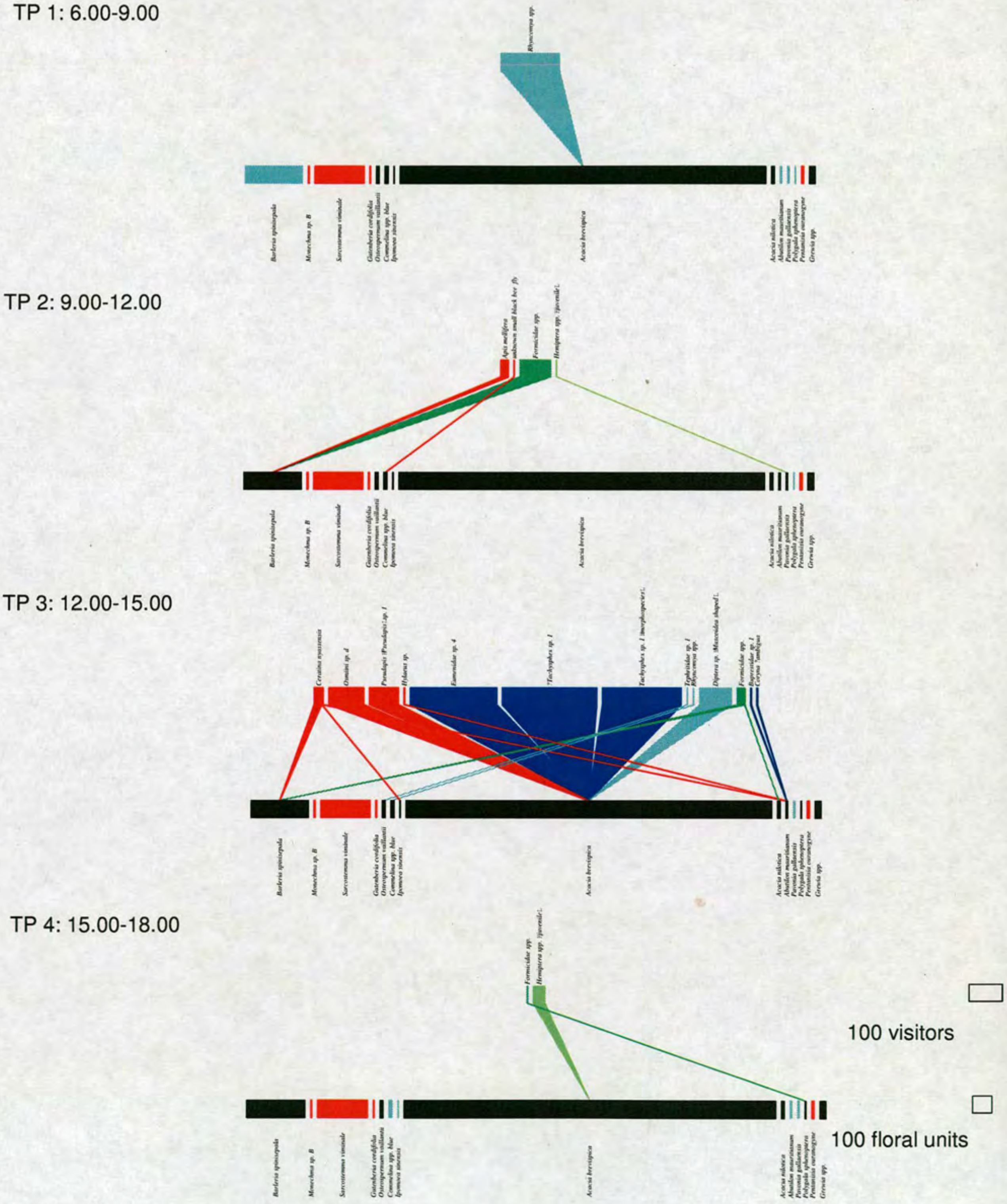


Figure 6.10 Flower-visitor interaction webs for each three hour time period at Turkana Boma in July. All webs are drawn to the same scale. Floral unit abundance is represented by the width of the bars on the bottom line, with observed species coloured black, unobserved species coloured red and species whose flowers were closed coloured blue. The relative frequency of visits by each visitor taxon is represented by a coloured bar on the top line. For further details refer to the legend for Figure 6.4.

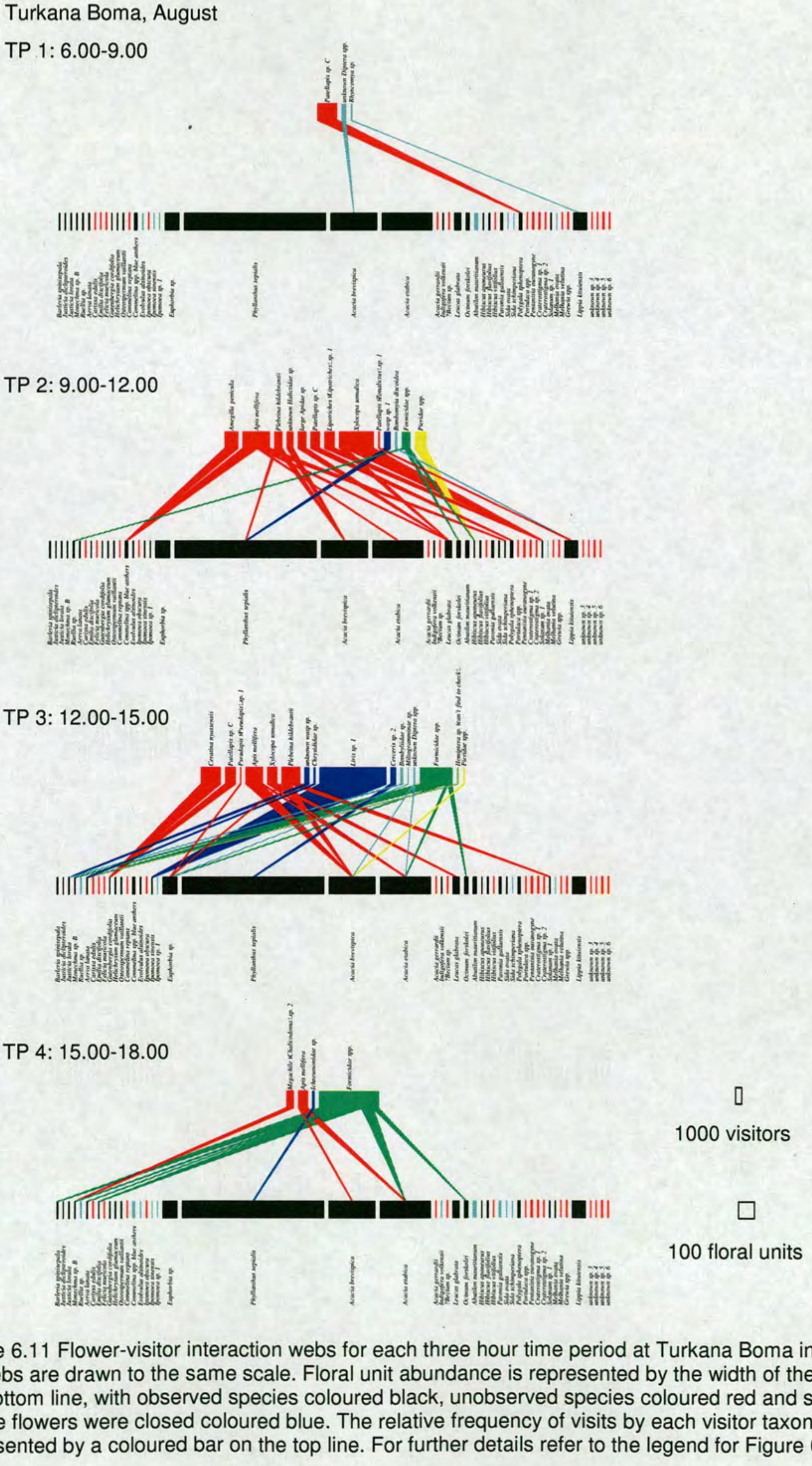
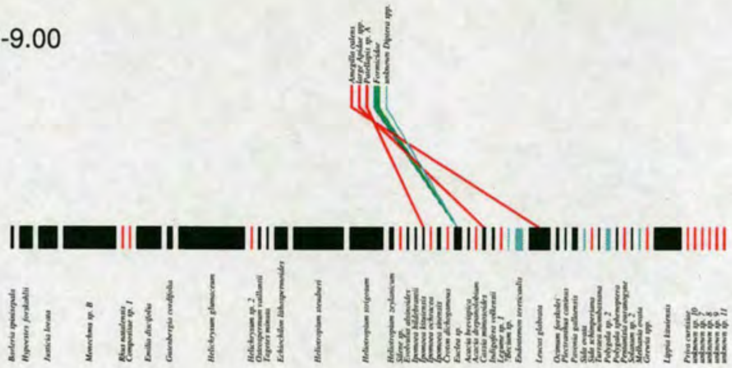


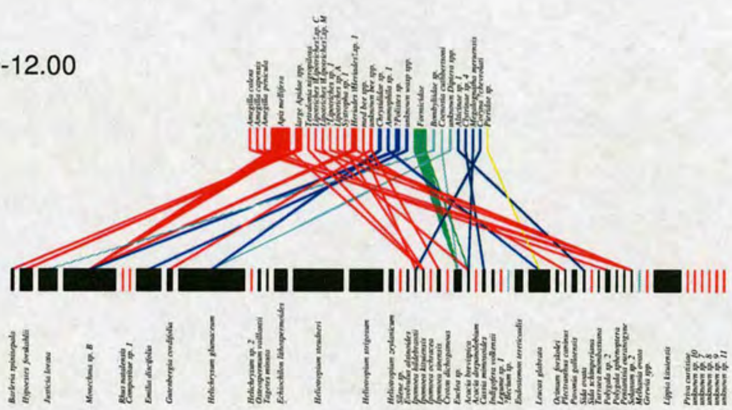
Figure 6.11 Flower-visitor interaction webs for each three hour time period at Turkana Boma in August. All webs are drawn to the same scale. Floral unit abundance is represented by the width of the bars on the bottom line, with observed species coloured black, unobserved species coloured red and species whose flowers were closed coloured blue. The relative frequency of visits by each visitor taxon is represented by a coloured bar on the top line. For further details refer to the legend for Figure 6.4.

Junction, June

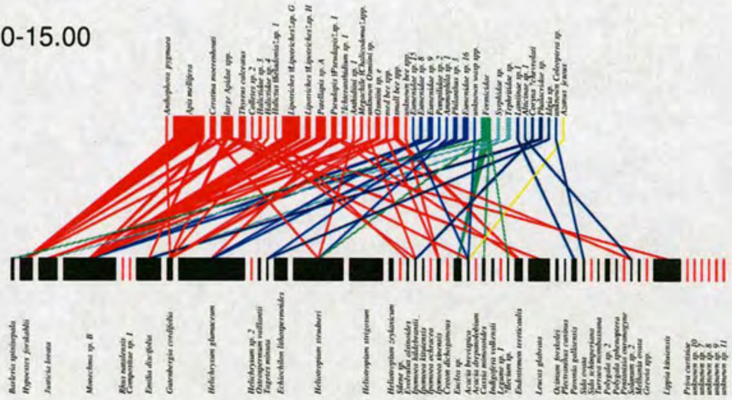
TP 1: 6.00-9.00



TP 2: 9.00-12.00



TP 3: 12.00-15.00



TP 4: 15.00-18.00

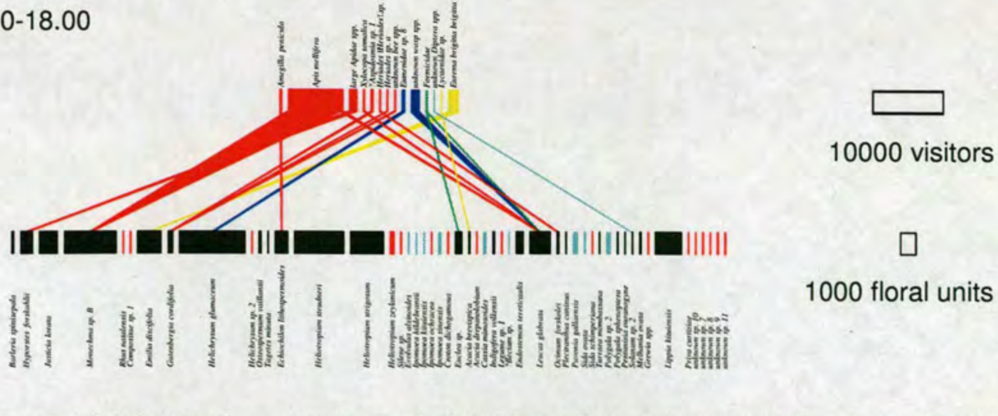
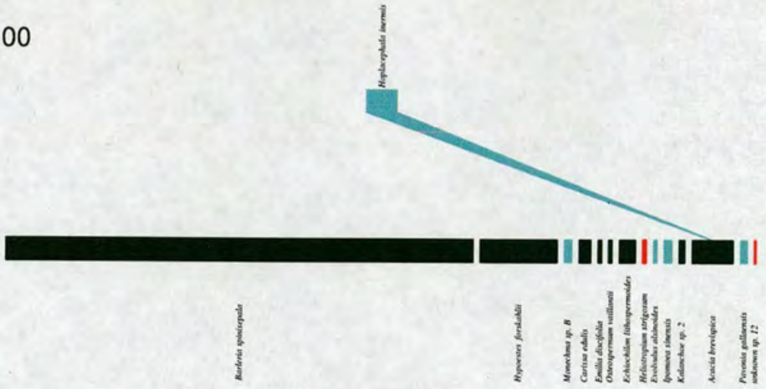


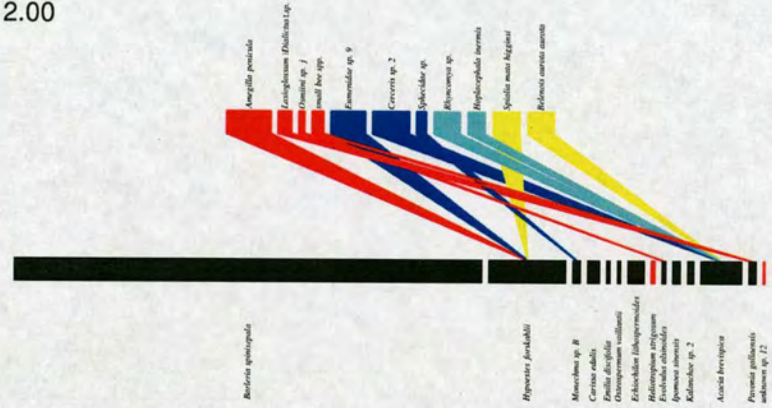
Figure 6.12 Flower-visitor interaction webs for each three hour time period at Junction in June. All webs are drawn to the same scale. Floral unit abundance is represented by the width of the bars on the bottom line, with observed species coloured black, unobserved species coloured red and species whose flowers were closed coloured blue. The relative frequency of visits by each visitor taxon is represented by a coloured bar on the top line. For further details refer to the legend for Figure 6.4.

Junction, July

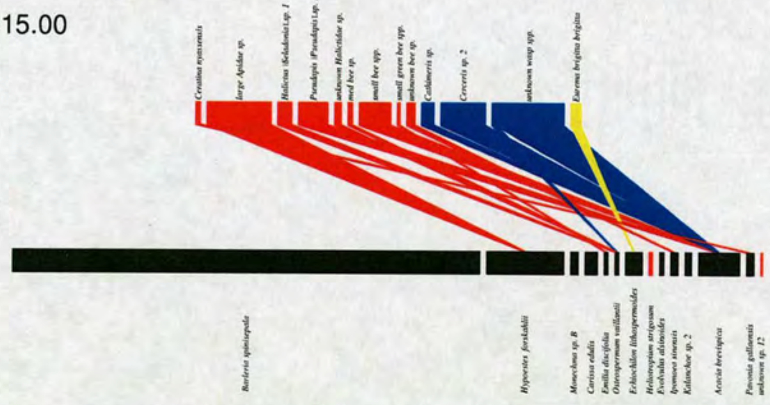
TP 1: 6.00-9.00



TP 2: 9.00-12.00



TP 3: 12.00-15.00



TP 4: 15.00-18.00

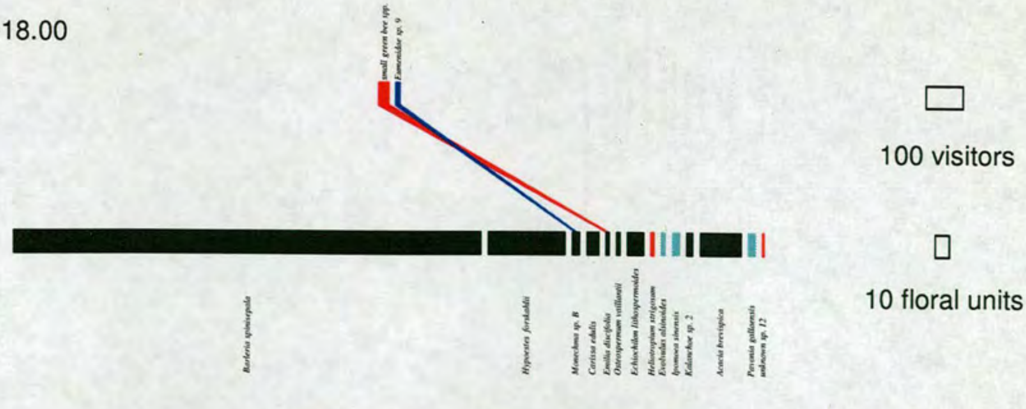
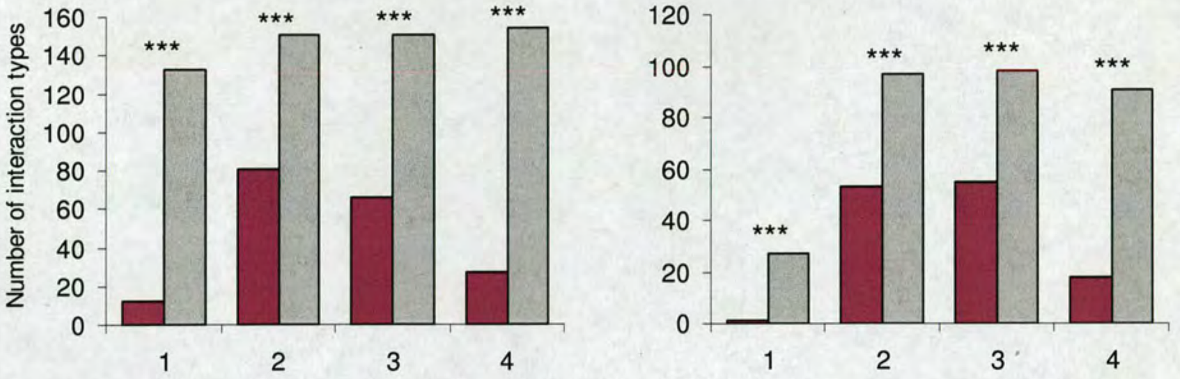
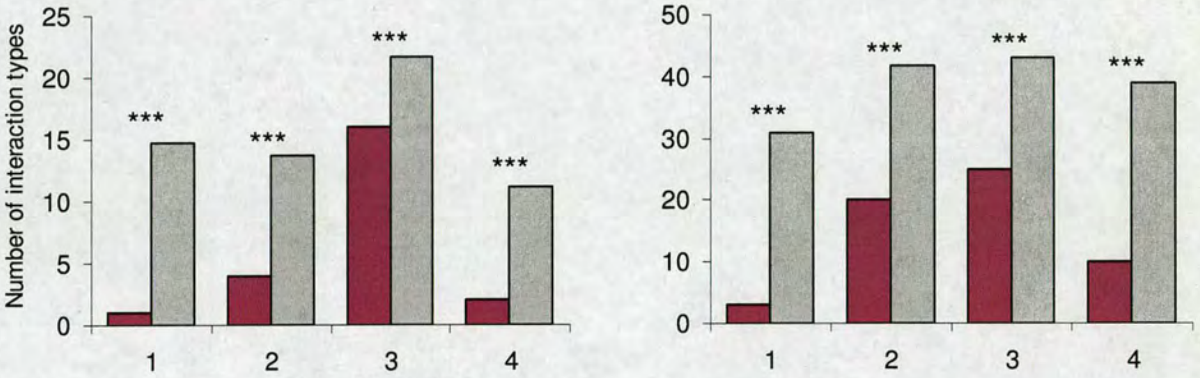


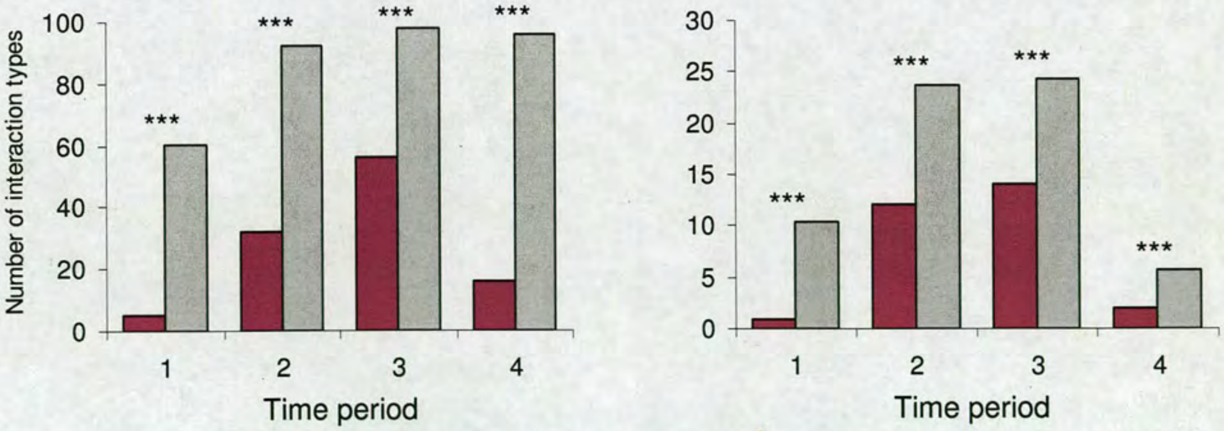
Figure 6.13 Flower-visitor interaction webs for each three hour time period at Junction in July. All webs are drawn to the same scale. Floral unit abundance is represented by the width of the bars on the bottom line, with observed species coloured black, unobserved species coloured red and species whose flowers were closed coloured blue. The relative frequency of visits by each visitor taxon is represented by a coloured bar on the top line. For further details refer to the legend for Figure 6.4.


(a) Turkana Boma, May (160)

(b) Turkana Boma, June (105)

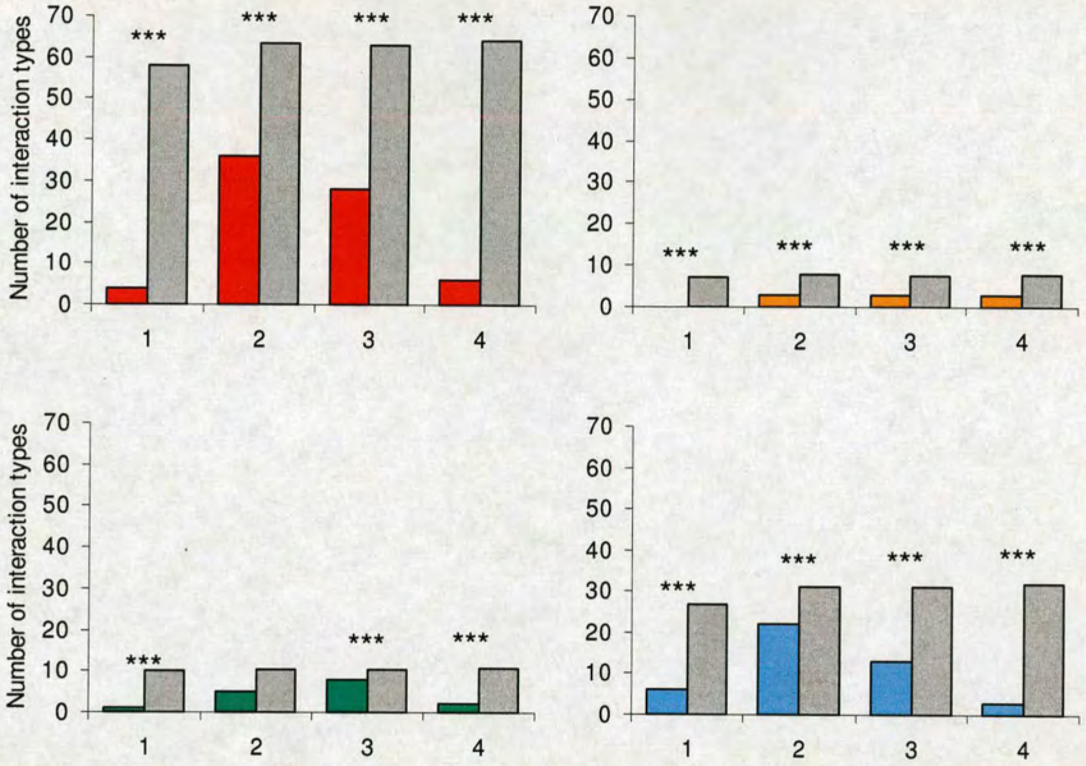

(c) Turkana Boma, July (22)

(d) Turkana Boma, August (46)


(e) Junction, June (99)

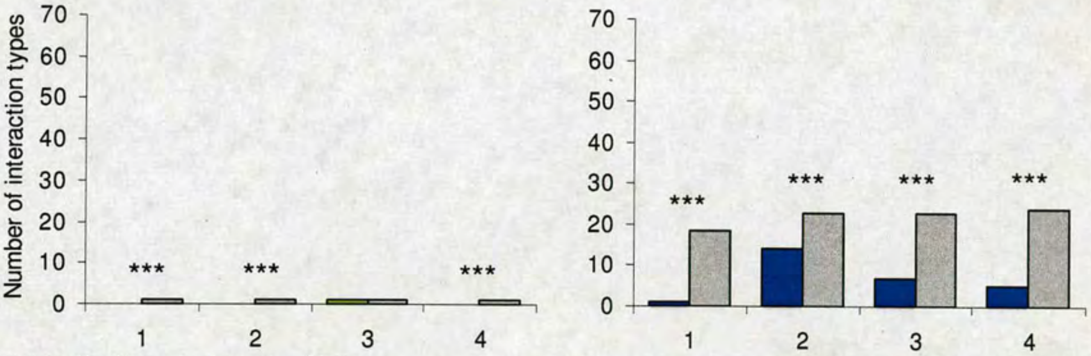
(f) Junction, July (26)

Figure 6.14 The number of interactions between plant species and visitor types for each time period for the observed webs (maroon) and the randomised webs (grey; mean shown) for all seasonal flower-visitor interaction webs. Asterices indicate whether the difference between the observed number of interactions for each time period is significantly different to those for the randomised webs. The total number of interaction types for each seasonal web is shown in brackets after each graph title.



(e) bugs (1)

(f) beetles (25)



(g) butterflies and moths (15)

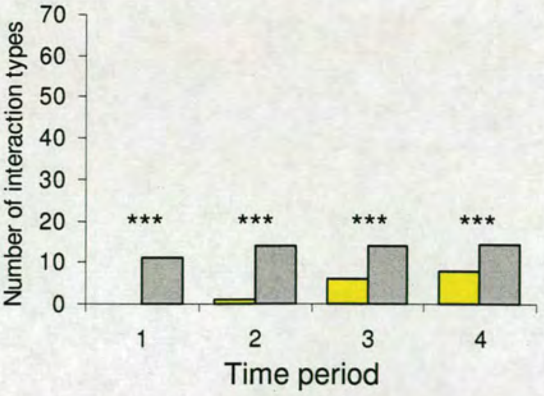
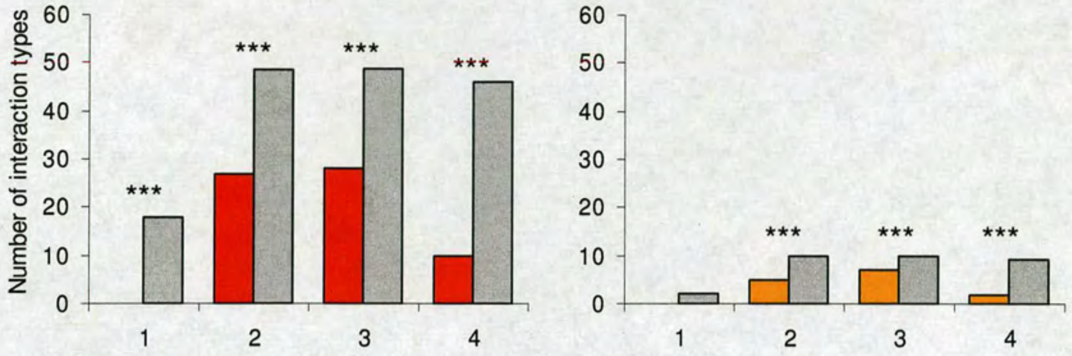


Figure 6.15 The total number of interactions for each visitor group in each time period for the observed webs (coloured) and the randomised webs (grey; mean shown) for Turkana Boma in May. Asterices indicate whether the difference between the observed number of interactions for each time period is significantly different to those for the randomised webs. The number of interaction types for each visitor group is shown in brackets after the graph title.

Turkana Boma, June

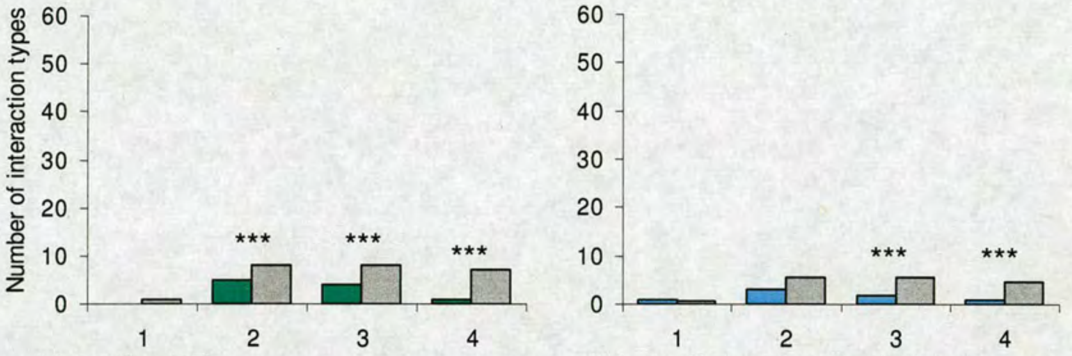
(a) bees (51)

(b) wasps (11)



(c) ants (9)

(d) flies (7)



(e) beetles (15)

(f) butterflies and moths (12)

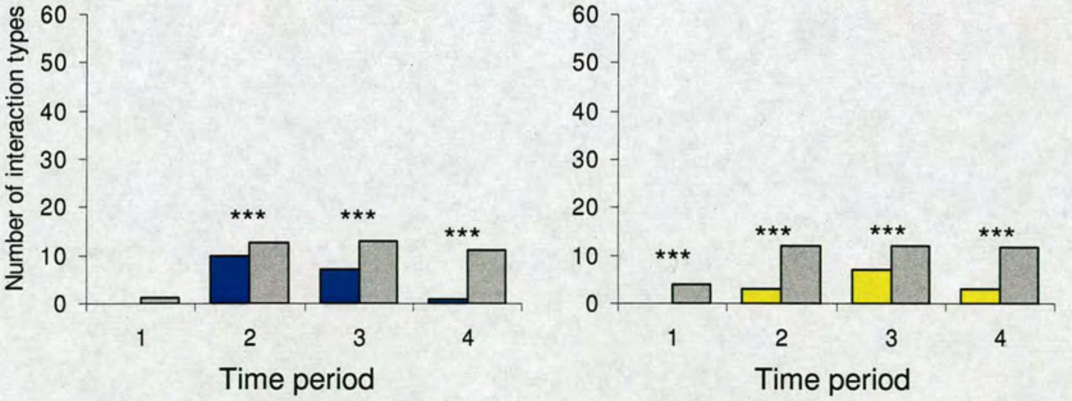


Figure 6.16 The number of interactions for each visitor group in each time period for the observed webs (coloured) and the randomised webs (grey; mean shown) for Turkana Boma in June. Asterices indicate whether the difference between the observed number of interactions for each time period is significantly different to those for the randomised webs. The number of interaction types for each visitor group is shown in brackets after the graph title.

Turkana Boma, July

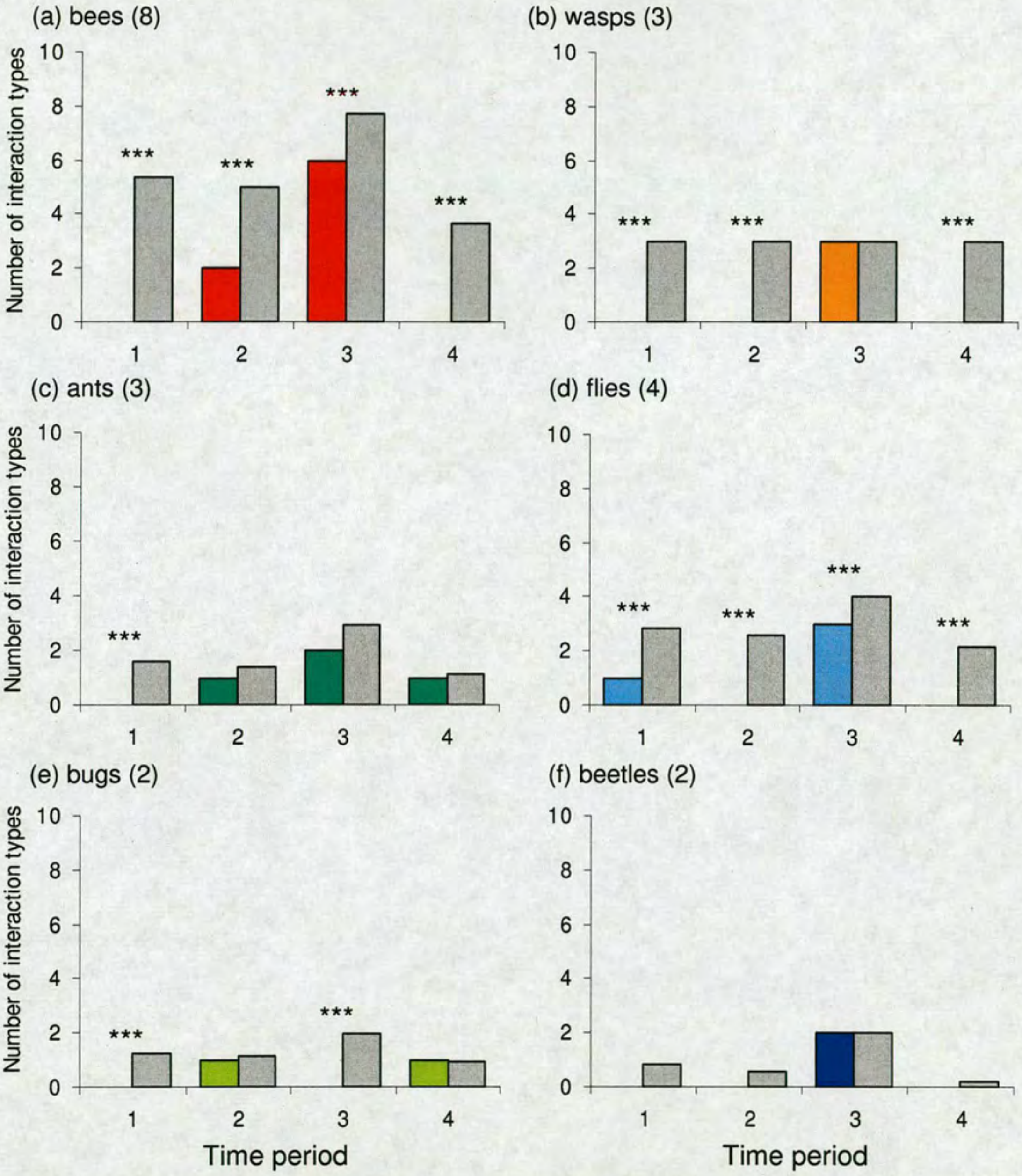
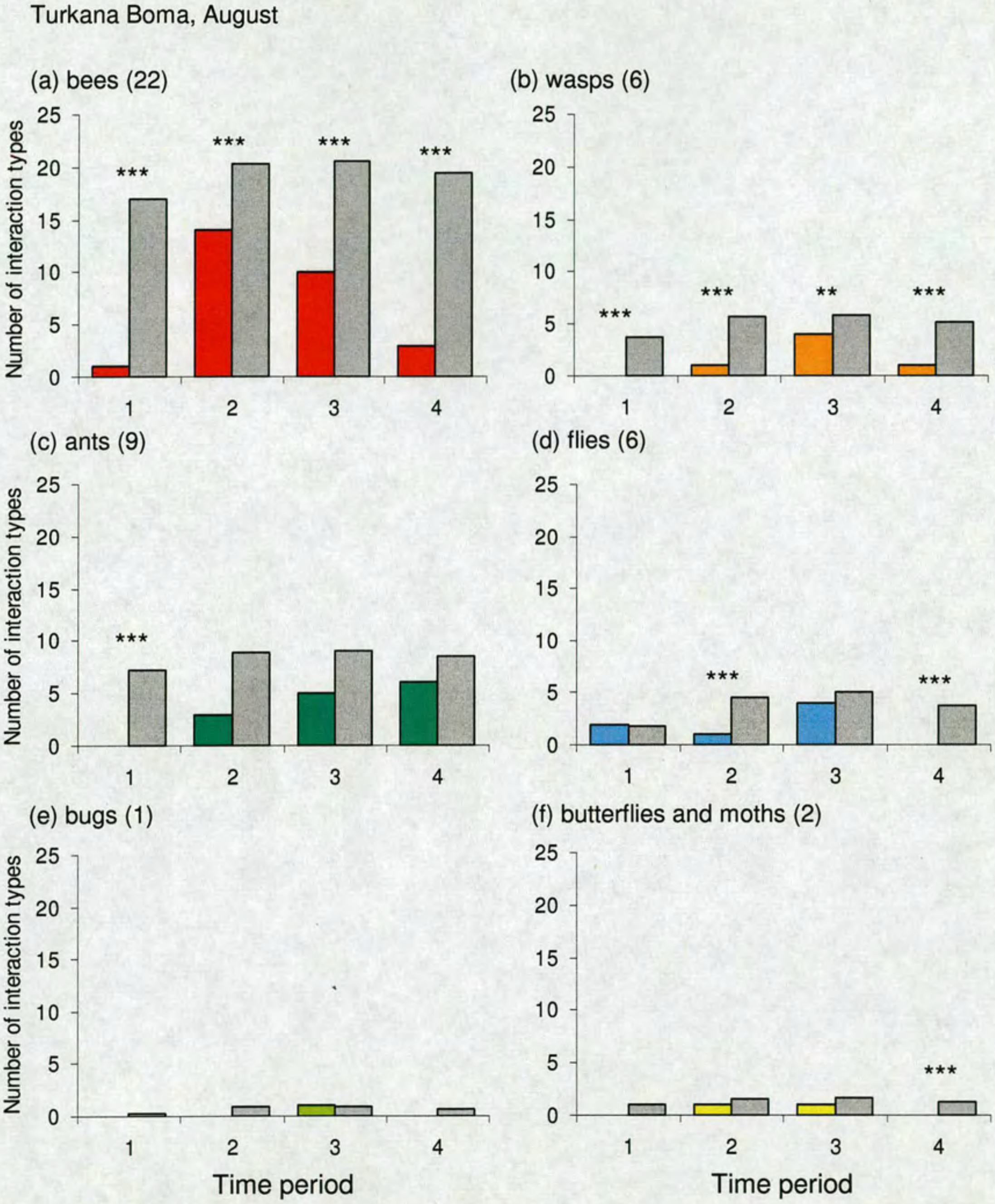


Figure 6.17 The number of interactions for each visitor group in each time period for the observed webs (coloured) and the randomised webs (grey; mean shown) for Turkana Boma in July. Asterices indicate whether the difference between the observed number of interactions for each time period is significantly different to those for the randomised webs. The number of interaction types for each visitor group is shown in brackets after the graph title.


Turkana Boma, August

(a) bees (22)

(b) wasps (6)

(c) ants (9)

(d) flies (6)

(e) bugs (1)

(f) butterflies and moths (2)

Figure 6.18 The number of interactions for each visitor group in each time period for the observed webs (coloured) and the randomised webs (grey; mean shown) for Turkana Boma in August. Asterices indicate whether the difference between the observed number of interactions for each time period is significantly different to those for the randomised webs. The number of interaction types for each visitor group is shown in brackets after the graph title.

Junction, June

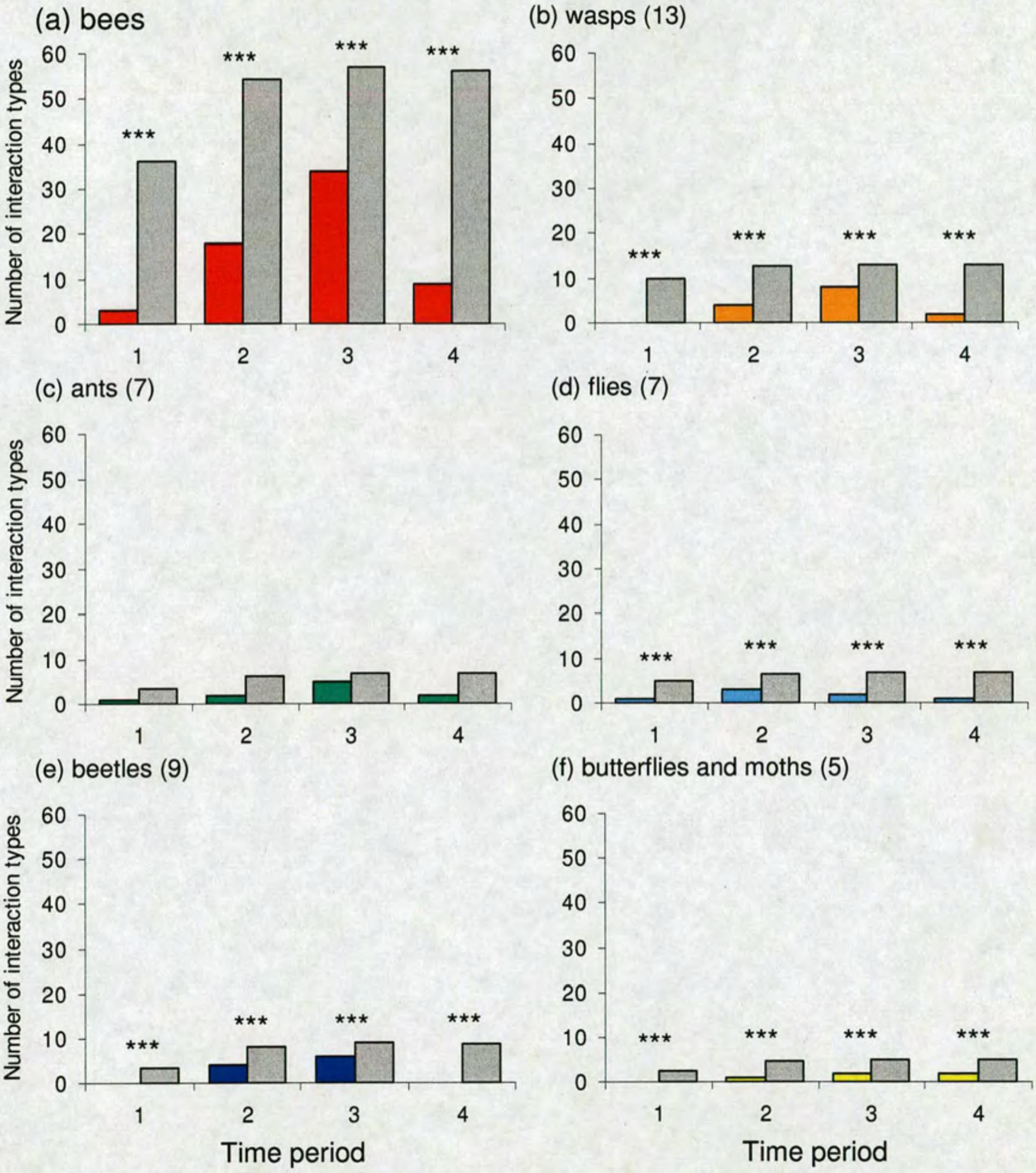


Figure 6.19 The number of interactions for each visitor group in each time period for the observed webs (coloured) and the randomised webs (grey; mean shown) for Junction in June. Asterices indicate whether the difference between the observed number of interactions for each time period is significantly different to those for the randomised webs. The number of interaction types for each visitor group is shown in brackets after the graph title.

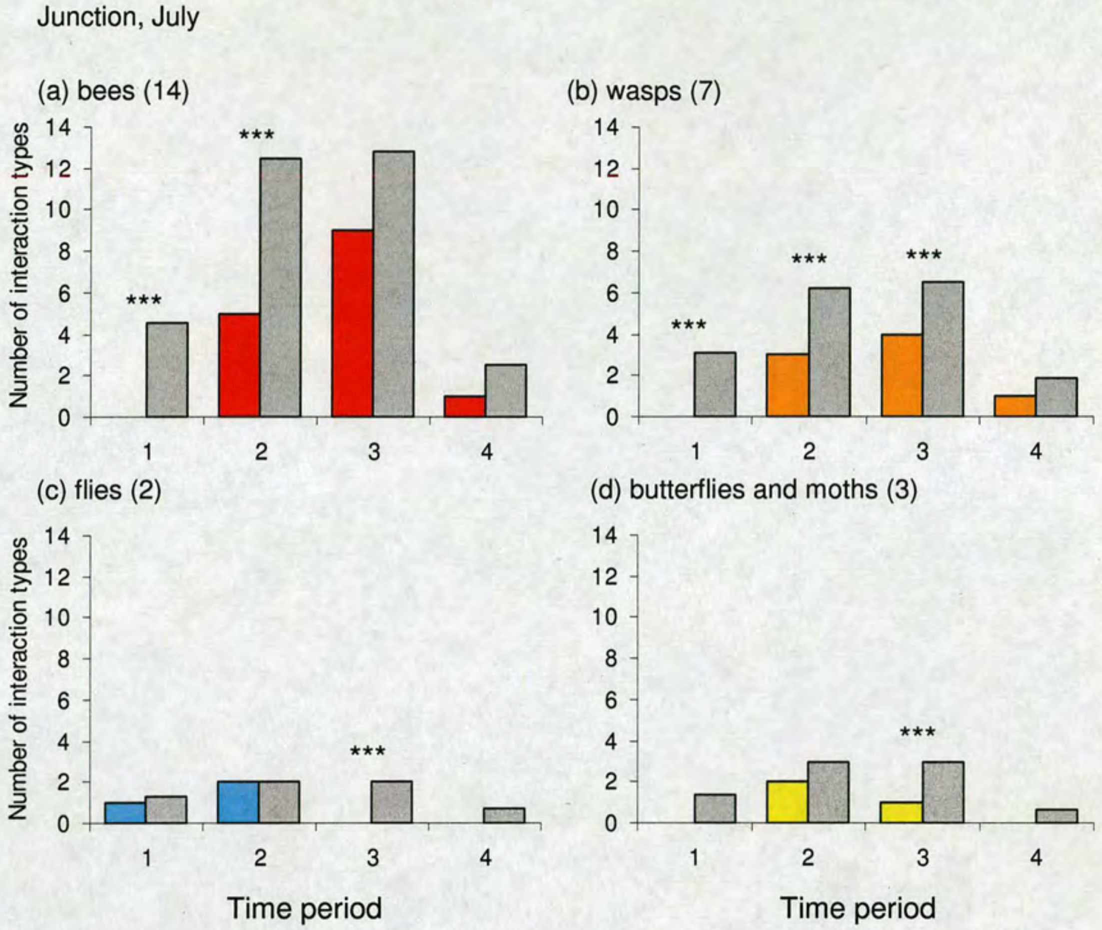


Figure 6.20 The number of interactions for each visitor group in each time period for the observed webs (coloured) and the randomised webs (grey; mean shown) for Junction in June. Asterices indicate whether the difference between the observed number of interactions for each time period is significantly different to those for the randomised webs. The number of interaction types for each visitor group is shown in brackets after the graph title.

### 6.3.4 Do plant species share visitors, and how are interactions of shared visitor species patterned through time?

Visitor species (including morphospecies) visited multiple plant species in all six seasonal webs (Table 6.7, Appendix 11). These consisted of 22 bee species, 6 fly species, 6 beetle species, 2 wasp species and 1 species of day flying moth (family Arctiidae). Six bee species visited multiple plant species in more than one seasonal web: *Pseudapis* (*Pseudapis*) sp. 1 (Halictidae), *Patellapis* sp. A (Halictidae), Osmiini sp. e (Megachilidae), *Heriades* (*Heriades*) sp. 1 (Megachilidae), *Megachile* (*Chalicodoma*) sp. 2 (Megachilidae) and *Apis mellifera* (Apidae).

Individual visitor species visited different plant species in different time periods in all webs except the July web at Turkana Boma (Table 6.7). These consisted of 17 bee, 4 fly, 6 beetle and 2 wasp species (Appendix 11). *Apis mellifera* visited different plant species across time periods in 4 webs (May, June and August at Turkana Boma and June at Junction) and *Heriades* (*Heriades*) sp. 1 visited different plants across time periods in two webs (June at Turkana Boma and Junction).

Individual visitor species visited multiple plant species during a single time period in all webs in July at Junction (Table 6.7). These consisted of 17 bee, 4 fly, 2 beetle and 1 moth species (Appendix 11). *Apis mellifera* visited multiple plant species in a single time period in four seasonal webs (May, June and August at Turkana Boma and June at Junction). *Heriades* (*Heriades*) sp. 1, *Pseudapis* (*Pseudapis*) sp. 1 and Osmiini sp. e each visited multiple plant species in a single time period in two seasonal webs (Appendix 11).

Table 6.7 Total identified visitor species (including morphospecies) in each web and the number observed visiting multiple plant species. Visitor species were active either in single time periods (TP) or multiple time periods. The table shows the number of visitor species that visited multiple plant species in a single time period and the number visiting different plant species in different times period. Some visitor species are included in both categories.

| Web | Total visitor species | Visiting multiple plant species | Present | | Visiting | |
|---|---|---|---|---|---|---|
| | | | in only 1 TP | in multiple TP | multiple plant species in a single TP | different species in different TP |
| Turkana Boma May | 58 | 20 | 6 | 14 | 14 | 14 |
| Turkana Boma June | 48 | 11 | 2 | 9 | 8 | 9 |
| Turkana Boma July | 10 | 1 | 1 | - | 1 | - |
| Turkana Boma August | 19 | 4 | 0 | 4 | 3 | 4 |
| Junction June | 51 | 11 | 3 | 7 | 5 | 7 |
| Junction July | 15 | 1 | 0 | 1 | 0 | 1 |

### 6.3.5 To what extent do acacias share visitors with other plants and how are interactions of shared visitor species with other plants patterned through time?

*Senegalia brevispica*, *V. etbaica* and *V. gerrardii* all shared visitor species or morphospecies with other flowering plant species in individual seasonal webs at Turkana Boma (Appendix 11). Although *S. brevispica* shared visitor types belonging to unidentified groups or morphogroups, no identified species or morphospecies were shared with other plant species in the same seasonal web at Junction. *Vachellia nilotica* did not share visitor species or morphospecies with other plant species and was visited by only two beetle morphospecies and ants. Only two *V. nilotica* flower heads were present on a single tree during any of the seasonal webs, therefore the observations during web sampling may not be representative of visits observed when flowering is greater. Visitors observed on *V. nilotica* flower heads during detailed observations included several species of *Megachile*. One of these, *Megachile* (*Chalicodoma*) sp. 2 visited 3 plant species in the seasonal webs at Turkana Boma.

*(a) S. brevispica*

*Senegalia brevispica* was visited by a wide diversity of visitor types in all seasonal webs (Fig. 6.2). In the May web at Turkana Boma, *S. brevispica* shared two bee, three fly and one moth species with other plant species within single time periods, and shared the same two bees, two of the flies and one beetle species with other plant species across time periods (Appendix 11). In total, *S. brevispica* shared visitors with seven plant species: *V. gerrardii*, *Melhania ovata* (Sterculiaceae), *Indigofera volkensii* (Fabaceae), *Ocimum forskolei* (Lamiaceae), *Croton dichogamus* (Euphorbiaceae), *Lippia kituiensis* (Verbenaceae) and Asteraceae spp. yellow.

In the June web at Turkana Boma, *S. brevispica* shared one bee species, *Lipotriches* (*Lipotriches*) sp. 1 (Halictidae), with *Abutilon mauritianum* (Malvaceae) and *Gutenbergia cordifolia* (Asteraceae) across time periods, and *Gutenbergia cordifolia* within the same time period (Appendix 11).

In the August web at Turkana Boma, *S. brevispica* shared two bee species, *Apis mellifera* and *Plebeina hildebranti*, with other plant species both within and across time periods (Appendix 11). *Apis mellifera* was shared with *V. etbaica*, both within and across time periods. In total, *V. brevispica* shared visitors with seven plant species: *V. etbaica*, *Solanum* sp. 1 (Solanaceae), *Phyllanthus sepialis* (Euphorbiaceae), *Euphorbia* sp. (Euphorbiaceae), *Sida schimperiana* (Malvaceae), *Commelina* spp. blue (Commelinaceae) and *Leucas glabrata* (Lamiaceae).

*(b) V. gerrardii*

In the May web at Turkana Boma, *V. gerrardii* shared one fly and one moth species within single time periods with other plant species, and the same fly and a beetle species across time periods with *S. brevispica* (Appendix 11). In total, *V. gerrardii* shared visitors with two plant species: *S. brevispica* and *Lippia kituiensis*.

*(c) V. etbaica*

In the August web at Turkana Boma, *V. etbaica* shared two bee species, *Apis mellifera* and *Xylocopa somalica*, both within and across time periods (Appendix 11). In total, *V. etbaica* shared visitor species with five plant species: *S. brevispica*, *Solanum* sp. 1, *Leucas glabrata*, *Sida schimperiana* and *Commelina* spp. blue

### 6.3.6 How do daily time periods differ in microclimate and are climatic differences across time periods correlated with variation in the visitors active in each time period?

At the beginning of time period 1 (6.00), temperatures were approximately 10°C and relative humidities between 70 and 80% (Fig. 6.21). During time period 1, temperatures increased to approximately 20°C and relative humidities decreased to between 40 and 60% by 9.00. During time period 2, temperatures increased to between 26 and 32 °C and relative humidities decreased to between 20 and 45% by 12.00. During time period 3 both temperature and relative humidities remained at similar levels. During time period 4 temperatures began to decrease and relative humidities began to increase. Temperature and relative humidities were not recorded after 17.00. Temperature and relative humidities varied across days and months, although followed the same pattern on all days shown in Fig. 6.21.

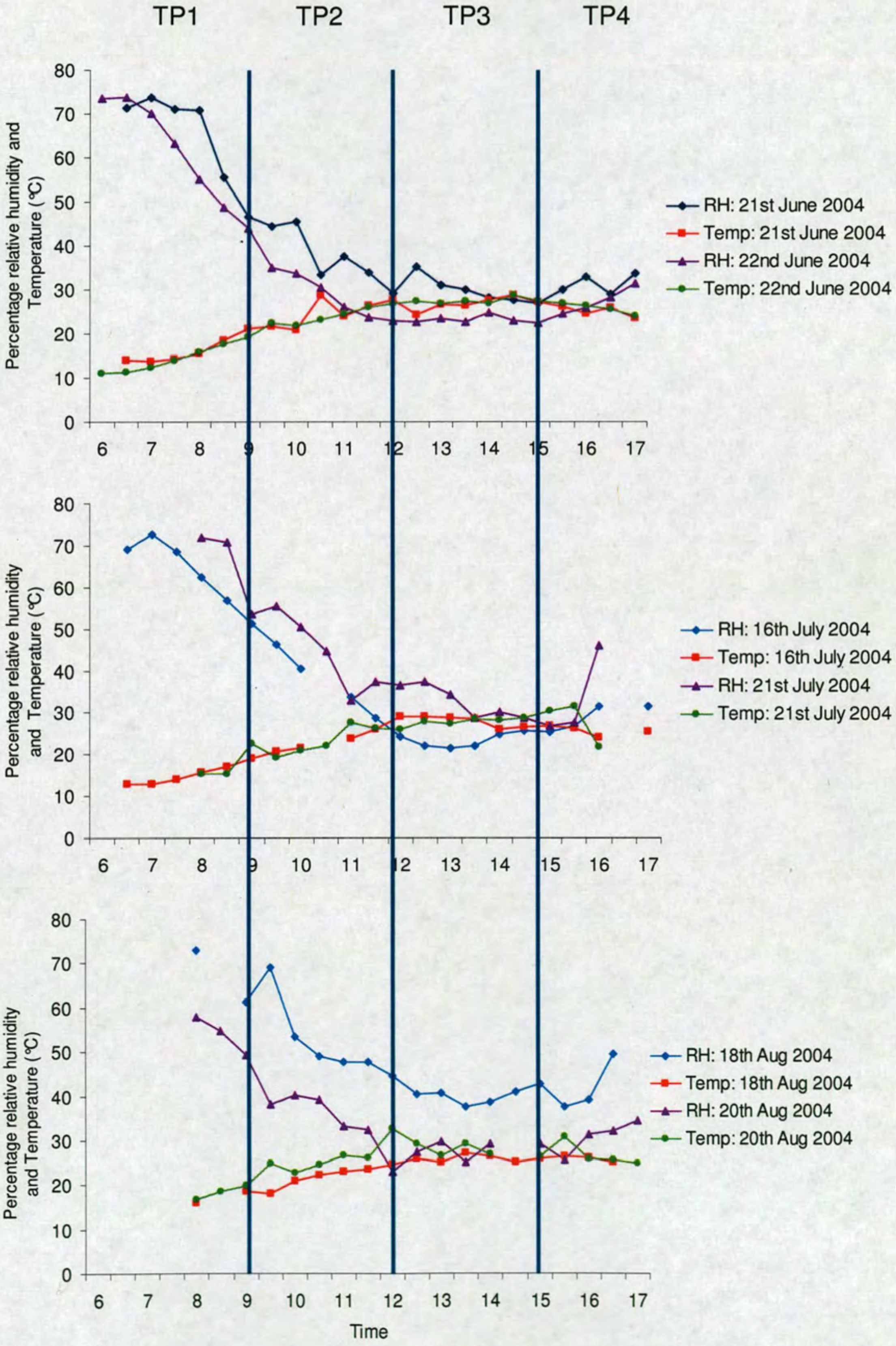


Figure 6.21 Daily patterns of temperature and relative humidity recorded at half-hourly intervals at Turkana Boma during the June, July and August web sampling.

Greater numbers of visits, and higher visitor diversities were observed during time periods 2 and 3. This six hour period incorporated the warmest temperatures and low relative humidities. In contrast, time period 1 was the coldest and most humid and fewer visitor types were observed. Time period 4 had relatively high temperatures, was slightly cooler than time period 3, but similar to time period 2. More visitor types were observed in time period 4 than in time period 1, although the diversity of visitors was not as high as in time periods 2 or 3.

## 6.4 Discussion

### 6.4.1 Critique of methods

*(a) Sampling effort*

This study aimed to sample entire flowering plant communities and their flower visitors to examine the extent to which interactions between them varied in seasonal and daily time. Sampling was designed so that as many plant species as possible could be observed in as short a time as possible in order to minimise the impact of seasonal variation on data collection for a single web. Each plant species was observed for a maximum of 1 hour 40 minutes in each seasonal web. These data were not as detailed as the visitation data collected for the acacia species in Chapter 5, but do allow comparisons of flower-visitor interactions across whole communities. In total, seventy-three plant species were sampled for 280 hours. This level of sampling compares favourably with those of previous plant-visitor community studies (Table 6.8).

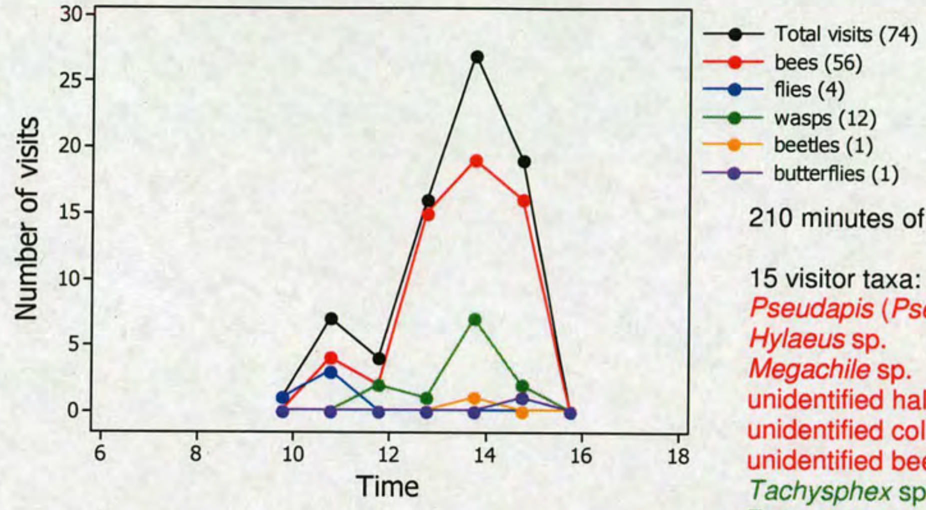
By collecting a relatively small amount of data for each plant species, it is inevitable that some interactions will have been missed. Acacias were sampled for floral visitors using two methods: (i) full day observations of the same set of flower heads (Chapter 5) and (ii) four 20 minute observations spread over a week during the community level studies (this chapter). The data collected during full day observations of acacias can be used to examine the extent to which data collected for the same species using the web methodology captured the overall visitor diversity and daily temporal visitation patterns.

The visitation data for *S. brevispica* in the July and August webs at Turkana Boma and for *V. etbaica* in the August web at Turkana Boma are compared to detailed observation days for the same species within or close to the web sampling times at Turkana Boma in Figs. 6.22-6.24. In general, the web observations preserved the daily patterns of visitation, but captured fewer visits and fewer taxa. However, the number of visitor taxa was the same in both the August web and on 6th September 2004, with a greater number of visits observed during the web sampling (Fig. 6.23). Furthermore, some visitors recorded during the web sampling were not observed on detailed observation days.

*(b) Null modelling approach*

The null modelling approach used in this study was developed to examine whether the number of interaction types per time period differed significantly between observed webs and those constructed from randomly assembled data. There were two assumptions in the model: (i) that the calculated interaction frequency remained the same in each time period and (ii) that the interaction types remained the same (i.e. no new links between plant and visitor species were made). The calculated interaction frequencies for each web were used to create randomised webs. Plants with high floral abundances involved in a large number of interaction types in the observed webs are likely to influence the results of the null model comparisons. If visitation to such plants is structured in daily time, the observed web is itself likely to be structured relative to the randomised webs. Similarly, if visitation to such plants is unstructured in daily time, strong temporal structuring in less abundant plants is unlikely to generate significant temporal structuring in the whole web. However, since plants with higher floral abundances had more floral resources, this might be an appropriate representation of daily flower-visitor interactions.

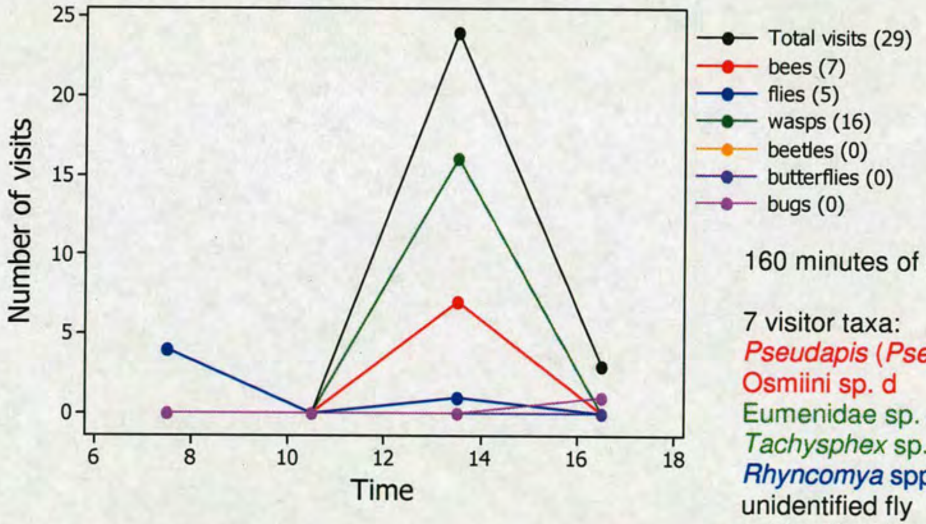
(a) Detailed observation data; 21st July 2004



210 minutes of sampling

15 visitor taxa:
*Pseudapis* (*Pseudapis*) sp. 1
*Hylaeus* sp.
*Megachile* sp.
unidentified halictid bee
unidentified colletid bee
unidentified bee
*Tachysphex* sp. 1
Eumenidae sp.
*Ammophila* sp.
*Oxybelus* sp.
*Rhyncomya* spp.
2 unknown flies
unidentified beetl
lycaenid butterfly

(b) Data from July web 2004

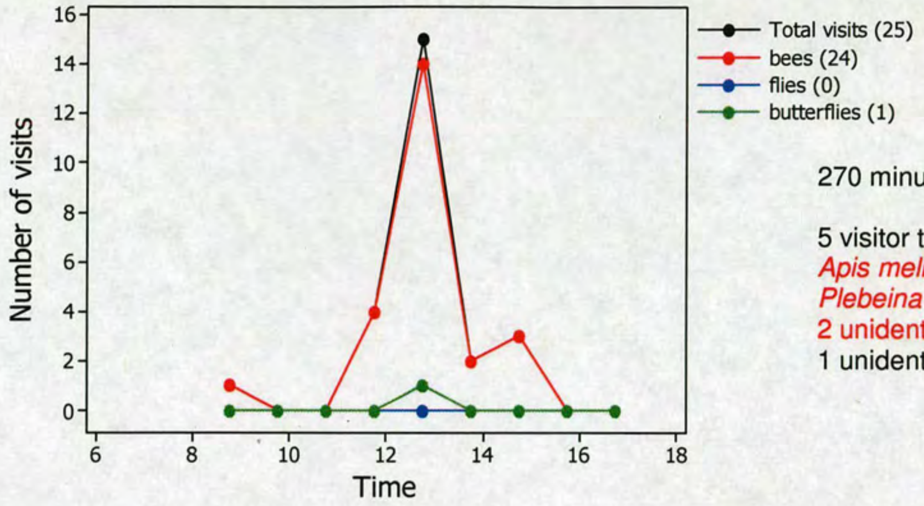


160 minutes of sampling

7 visitor taxa:
*Pseudapis* (*Pseudapis*) sp. 1
Osmiini sp. d
Eumenidae sp. 4
*Tachysphex* sp. 1
*Rhyncomya* spp.
unidentified fly
unidentified bug

Figure 6.22 Patterns of visitation for *S. brevispica* (a) on 21st July 2004 and (b) during the July web at Turkana Boma in 2004. In (b) the data are plotted mid-way through each time period. Total visits for each visitor group are shown in brackets. Total observation time and number of visitor taxa are given, bees are in red, wasps in green and flies in blue. All other taxa are in black.

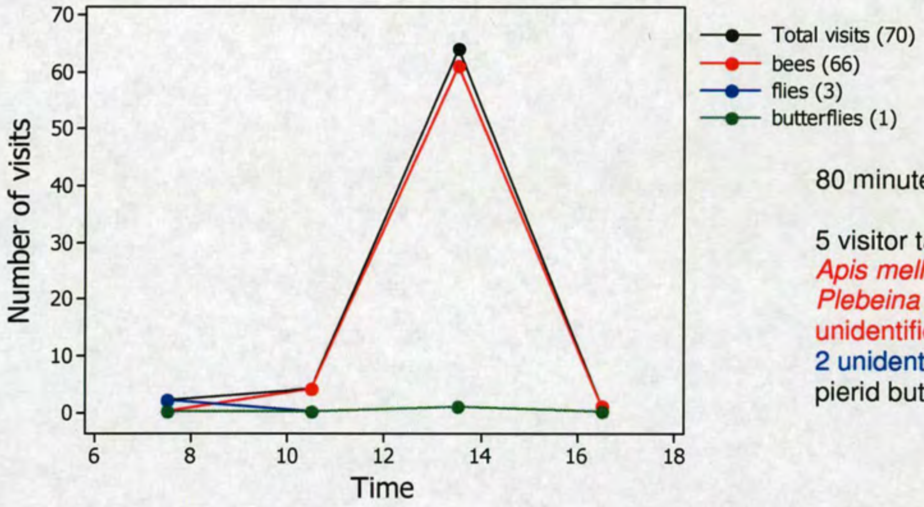
(a) Detailed observation data collected on 6th September 2004



270 minutes of sampling

5 visitor taxa:
*Apis mellifera*
*Plebeina hildebranti*
2 unidentified bees
1 unidentified butterfly

(b) Data from August web 2004

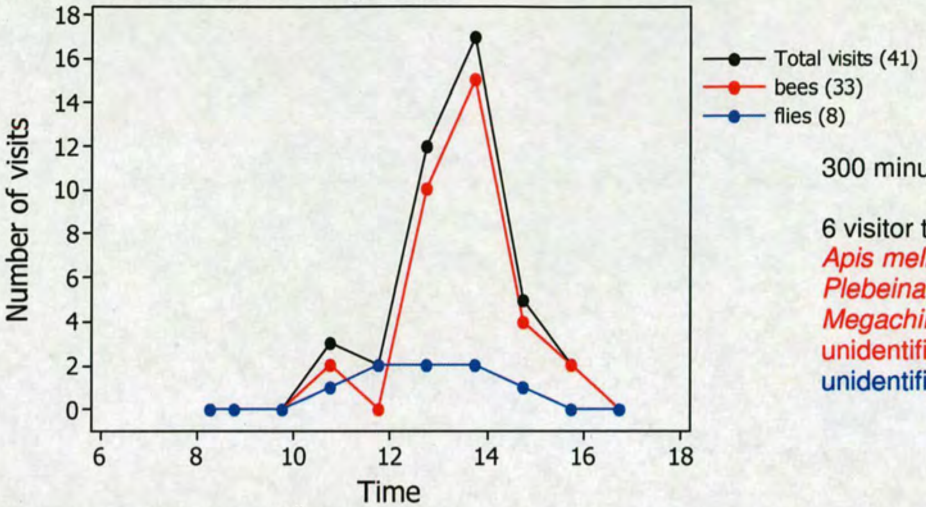


80 minutes of sampling

5 visitor taxa:
*Apis mellifera*
*Plebeina hildebranti*
unidentified halictid
2 unidentified flies
pierid butterfly

Figure 6.23 Patterns of visitation for *S. brevispica* (a) on 6th September 2004 and (b) during the August web at Turkana Boma in 2004. Total visits for each visitor group are shown in brackets. In (c) the data are plotted mid-way through each time period. Total observation time and number of visitor taxa are given, bees are in red and flies in blue. All other taxa are in black.

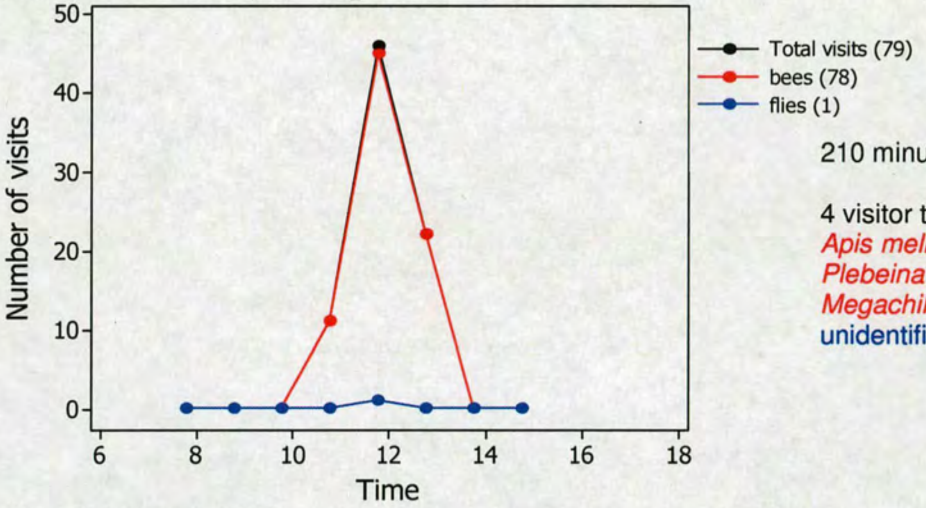
(a) Detailed observation data; 21st August 2004



300 minutes of sampling

6 visitor taxa:
*Apis mellifera*
*Plebeina hildebranti*
*Megachile* sp.
unidentified halictid
unidentified fly

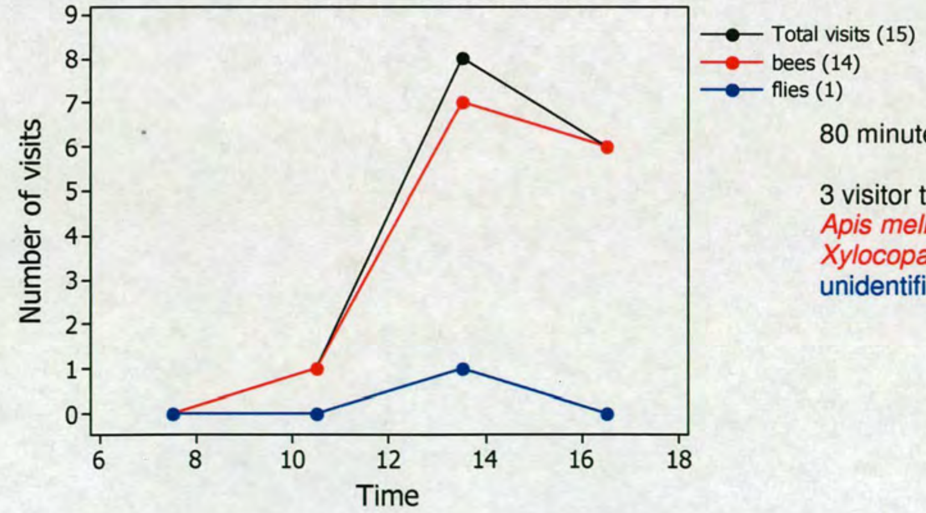
(b) Detailed observation data; 27th August 2004



210 minutes of sampling

4 visitor taxa:
*Apis mellifera*
*Plebeina hildebranti*
*Megachile* sp.
unidentified fly

(c) Data from August web 2004



80 minutes of sampling

3 visitor taxa:
*Apis mellifera*
*Xylocopa somalica*
unidentified fly

Figure 6.24 Patterns of visitation for *V. etbaica* (a) on 21st August 2004, (b) on 27th August 2004 (c) during the August web at Turkana Boma in 2004. Total visits for each visitor group are shown in brackets. In (c) the data are plotted mid-way through each time period. Total observation time and number of visitor taxa are given, bees are in red and flies blue. All other taxa are in black.

*(c) Taxonomic resolution*

Despite best efforts to catch flower visitors, not all were identified to species. A large proportion of visitors were identified to species or morphospecies (59%), with the remainder grouped to order (17%) or family level (morphogroups; 26%). This is a respectable achievement given that the taxonomy for many insect groups in this region is limited. Furthermore, identifications to genus or species often required the expertise of specialised taxonomists and even then it was not always possible to assign a species name to specimens. These data were sufficient to identify patterns in daily time for visitor groups and also allowed the identification of shared visitor species and the distribution of their visits to different plant species in daily time.

Although the results of this study should be interpreted with a degree of caution regarding species-level interactions, these data show how flower visits by major visitor groups (e.g. bees, wasps, flies) varied across daily and seasonal time in two savannah flowering plant communities. This study represents the first community-level study of plant-visitor interactions in an African savannah habitat and is the first study to incorporate comparisons of interactions on a daily timescale for entire plant-visitor communities.

### 6.4.2 Variation in plant-visitor interactions across seasonal time and across sites

The diversity of plants and visitors varied across seasonal time at both Turkana Boma and Junction, with higher diversities in months that followed rainfall (May, June and August) and lower diversities during July, the driest month. The diversities of flower-visitor interactions were greater in months with more plant species, although this could have been a sampling artefact. The species composition of the flowering plant communities also varied across seasonal times at both sites, although most plant species were present in more than one web at each site.

The identities of flowering plant species varied between sites, with approximately half of those at Junction also found at Turkana Boma, which was the more diverse site. Similarly, approximately half of the visitor types at Junction were also found at Turkana Boma, although the similarity might have been higher if all visitors could have been identified to species. Although community composition varied between the two sites, plant and visitor diversities were similar at Turkana Boma and Junction when both communities were studied simultaneously (Table 6.1).

The main visitor groups (bees, wasps and flies) and the relative diversity of their interaction types were similar across all webs at both sites (Figs. 6.4-6.6). Bees were the most diverse visitor group and responsible for the most interaction types in all webs.

Individual plant species present in multiple webs at each site had different flower visitors at different seasonal times. This could have been because different visitor species were active at different seasonal times or because the level of sampling did not pick up the full range of visitors (see section 6.4.1). Identified visitor species active across seasonal webs at each site visited different plant species in different webs. Such patterns are consistent with the idea of pollinator partitioning in seasonal time. However, visitor species active in multiple webs were often observed visiting different plant species, despite the presence of plants they had visited in other webs. The composition and frequency of visitors to individual plant species could depend on the abundance of other flowering plant species at a particular seasonal time and location. Visitors might choose to forage on a particular species because it offers a better quality of floral reward (Roubik 1989). More detailed studies of visitation at different seasonal times could reveal whether the visitor composition for individual plant species does change throughout the season, or whether the results in this study were due to low sampling effort.

In each seasonal web, the linkage levels for visitor types were generally lower than those for plant species. These findings are consistent with previous studies of plant-visitor communities which have typically found that plant species are more generalised (i.e. have more links) than visitors (e.g. Dicks et al. 2002, Olesen et al. 2002, Lundgren and Olesen 2005, Petanidou and Lamborn 2005). However, since a proportion of visitors were not identified beyond family or order the actual linkage levels for both groups could have been higher.

A large proportion of plant species and visitor types had only one partner species in each seasonal web (Figs. 6.2, 6.3). Whilst it is possible that specialised relationships between plants and pollinators existed in the two communities, it is more probable that the level of sampling did not reveal further interactions. When interaction types were considered across all seasonal webs, most plant species with a single link in an individual web were visited by a wider range of visitors, and an increased number of visitor types were found on multiple plant species. Only six plant species in this study were visited by a single visitor type: *Craterostigma* sp. 1 (Scrophulariaceae), *Kalanchoe* sp. 1 (Crassulaceae), *Melhania velutina* (Sterculiaceae), *Polygala* sp. 2 (Polygalaceae), *Ruellia* sp. (Acanthaceae) and *Sida schimperiana* (Malvaceae). All of these species received a relatively small number of observations because either they flowered during few of the seasonal webs or had open flowers in only one or two time periods.

If the results are representative of the two flower-visitor communities studied, this suggests that shared visitors might be structured in seasonal time. More detailed studies of individual plant species are required to determine whether sampling effort in this study was adequate for all species in these communities.

Only one previous study has considered plant-pollinator communities over an extended seasonal timescale. Basilio et al. (2006) examined monthly flower-visitor interaction webs over 3 years. Similarly, they found that visitor and interaction diversities were higher when more plant species were flowering. Basilio et al. concluded that the examinations of flower-visitor interactions over extended seasonal time should consider consecutive individual webs rather than cumulative webs incorporating all data, in order to understand the role and importance of different species in the community.

### 6.4.3 Are interactions in seasonal webs structured in daily time?

In all seasonal webs, flower-visitor interactions varied in daily time and different visitors were active at different times during the 12-hour sampling period (Figs. 6.8-6.13). The results of the null model analyses show that the number of interaction types in each time period was lower than in random communities composed from the same plant-visitor interactions in all seasonal webs at both sites (Fig. 6.14). This result arises because particular interactions occurred in specific time periods, rather than throughout the entirety of the 12-hour sampling period. Bees were the only visitor group which consistently followed the same pattern as the overall data, and were therefore the most consistently time structured visitors.

All visitor groups demonstrated similar patterns of diversity in visitor types and interaction types through the four daily time periods; diversities were generally higher in time periods 2 (9.00-12.00) and 3 (12.00-15.00), lower in time period 4 (15.00-18.00) and lowest in time period 1 (6.00-9.00). Wasps, butterflies and moths were not observed visiting flowers in time period 1, whilst beetle visitors were seldom observed during this time period.

At least some of the observed structure is due to bottom-up influences of flower opening times. The flowers of several plant species in each seasonal web were closed during at least one time period (Figs. 6.7-6.13). Consequently these plant species could only be visited in time periods in which their flowers were open. Bottom-up structuring will also affect daily patterns of flower visitation through the timing of pollen and nectar presentation, which was not examined in this study. This was shown clearly for the acacias in Chapter 5, with visitors, especially bees, closely tracking pollen availability. Examination of daily resource availability for more plant species could provide additional support for the existence of bottom-up structure in these communities. Previous studies have shown that the availability of floral resources is an important determinant of flower-visitor community structure, particularly bees (Potts et al. 2003, 2004), and pollen and nectar availability on a daily timescale is likely to be an important factor in the timing of flower visits by pollinators.

Although no previous plant-visitor community studies have considered the variation of flower-visitor interactions in daily time, most recent studies have sampled for flower visitors over a broad daily time window (Table 6.8). In the majority of studies it is unclear whether each plant species was observed throughout the specified ranges, and only Stang et al. (2006) specified that observations for all species were spread throughout their sampling window. The necessity of considering flower-visitor interactions over daily time will depend on the focus of the study. However, any studies considering the potential for competitive or facilitative interactions among plant species should consider the activity of shared pollinators over a daily timescale to avoid misinterpretation.

Table 6.8 Comparisons of sampling methods and sampling effort in recent web-based flower-visitor community studies

| Study | Habitat | Location | Sampling dates | Sampling method | Sampling effort | Times of sampling | Plant species | Visitor species |
|---|---|---|---|---|---|---|---|---|
| Memmott 1999 | meadow | UK | July 1997 | transects | not specified | not specified | 26 | 79 |
| Dicks et al. 2002 | two sites: hay meadows | UK | 14 April-16 July year unknown | transects | fortnightly or weekly | Three per day 9.00-10.30, 12.30-14.00, 16.00-17.30 | 21<br>29 | 61<br>36 |
| Dupont et al. 2003 | sub-alpine desert | Tenerife, Canary Islands | 7 May - 7 June 2001 | 5-20 min observations, repeated at different times of day | 15 days, 145 hours, each plant species was observed for >1 hr | 7.00-21.00, although mainly 10.00-17.00 | 11 | 38 |
| Forup and Memmott 2005 | four sites: hay meadows | UK | May-July 2000 | transects | fortnightly per site | not specified | 42 | 85 |
| Lundgren and Olesen 2005 | heath and bare rock | Greenland | 1 July-4 August 2002 | 20 min observations | total ~4 h per plant species | 10.00-16.00 | 17 | 149 |
| Basilio et al. 2006 | talar forest | Argentina | August 1998-May 2001 | transects | monthly<br>560 hours | morning-dusk | 37 | 101 |
| Gibson et al. 2006 | five sites: farmland/grassland | UK | June-September 2002<br>June-September 2003 | 15 min observations | not specified | not specified | not given | not given |
| Hegland and Totland 2006 | grassland/meadow | Norway | 28 May- 18 Aug 2003 | 10 min observations | 201 censuses (33.5 hours) | 10.00-16.00 | not given | not given |
| Morales and Aizen 2006 | four sites: forest habitat | Chile | 2000-2001 | 15 min observations | 1639 censuses (342.25 hours) | 9.00-18.00 | 28 | 110 |
| Stang et al. 2006 | Mediterranean vegetation mosaic | Spain | March-April 2003 | 15 min observations | 4 x 15 min per plant, spread throughout the day | 10.00-18.00 | 25 | 111 |

### 6.4.4 Daily temporal patterns of shared visitor species

If visitation by shared pollinators is structured in daily time in these communities, shared visitors will visit different plant species at different times of day. Between 10% and 40% of visitor species and morphospecies visited multiple plant species in all seasonal webs (Table 6.7).

Shared visitor species and morphospecies were observed on different plant species in different time periods in all seasonal webs apart from July at Turkana Boma (Table 6.7). If these visitors are important pollinators for at least one plant species visited in each time period, this pattern would be consistent with the idea that plants could be partitioning pollinator visits in daily time in these communities.

Shared visitor species also visited different plants within single time periods in all seasonal webs apart from the July web at Junction. Plant species might compete for visits from these species if they are important pollinators, although partitioning in daily time could be occurring on finer timescales than can be detected in this study, or partitioning could be by other means, such as pollen placement on pollinator bodies.

More information is needed regarding which visitors could be important pollinators for plant species sharing visitors in this community, to establish whether plants might benefit from partitioning visits in daily time to avoid competition for pollinators. Data for the relative frequencies of interactions were limited because of the large number of plant species sampled in this study. A more accurate estimation of the frequency of visits by shared visitors to individual plant species would demonstrate whether shared visitors observed in this study could be important pollinators, or were simply incidental visitors. Visitors carrying pure pollen loads of single plant species are more likely to be effective pollinators for that species. Therefore examination of the pollen loads of shared visitors would further demonstrate which visitors have the potential to successfully pollinate which plant species.

### 6.4.5 To what extent do acacias share visitors with other plants and how is shared visitor activity patterned through time?

Four acacia species, *S. brevispica*, *V. gerrardii*, *V. etbaica* and *V. nilotica* were included in the webs at Turkana Boma, whilst only *S. brevispica* was sampled in the Junction webs. Other acacia species were either not present in the plots, or did not flower during web sampling. *Senegalia brevispica*, *V. gerrardii* and *V. etbaica* received visits from a wide diversity of visitor types in each seasonal web in which they were sampled and all shared visitor species and morphospecies with other plants at Turkana Boma (Appendix 11). Sampling was not representative for *V. nilotica* during web sampling as only two flower heads were present at any time.

*Senegalia brevispica*, *V. gerrardii* and *V. etbaica* all shared visitor species and morphospecies with other plants across time periods and within single time periods (Appendix 11). *Senegalia brevispica* and *V. etbaica*, in particular, shared visitors with a wide diversity of plant species. All three acacias also shared visitors with other acacias in the same seasonal web.

The detailed studies in Chapter 5 showed that all four acacias sampled in the webs shared a wider diversity of flower visitors with other plant species than was shown by the webs (Appendix 6). In addition, *V. drepanolobium* and *S. mellifera*, which were not included in the webs, also shared visitor species with plant species sampled in the webs. In total, these studies revealed that acacias shared visitor species with an additional 27 plant species in the webs. However, the detailed studies were carried out over a two year period and across several sites at Mpala, and further examination of particular flower-visitor communities would be required to establish the extent to which these visitors are shared in daily time.

Partitioning on a daily timescale will only occur for visitors that are important pollinators for multiple plant species. The importance of each visitor type as pollinators for either the acacias or plant species with which they shared visitors is not known in this study; sampling time per plant species was limited and no information on pollen loads carried by visitors is available. The evidence for daily temporal partitioning of acacia visitors among acacias and other flowering plant species in this study is limited. Although acacia visitors were shared with other plant species in several webs, these visitors were often observed on different plant species in the same time period (Appendix 11). Partitioning could be occurring on a finer timescale than can be detected using the time periods in this study, or might involve a limited number of visitor taxa that were not adequately sampled. Further studies of the visitor assemblages and patterns of visitation for the plants with which acacias share visitors are needed to establish whether acacias partition shared pollinators in daily time with other plants in theses communities.

### 6.4.6 Variation of visitor activity with climatic differences across time periods

Temperature and relative humidity varied throughout the 12-hour sampling day (Fig. 6.21). Time period 3 incorporated the warmest and least humid part of the sampling day. Numbers of visits and the diversities of visitor and interaction types were highest in time periods 2 or 3. Although temperature and relative humidity were similar between time periods 2 and 4, numbers of visits and visitor and interaction type diversities were lower in time period 4. Time period 1, the coldest part of the sampling day, had fewest visits and the lowest diversity of visitor and interaction types.

We might expect more visitors to be active in the warmer time periods in these communities since the activity patterns of many insect taxa are limited by temperature (e.g. Gilbert 1985, Willmer 1985, Strohm and Linsenmair 1998, Orueta 2002, Willmer and Stone 2004). In this study, two visitor groups, wasps and lepidopterans (butterflies and moths), were not observed during time period 1. The most consistently active group in this time period across seasonal web were flies, although many of these were immobile and remained on single flowers.

Large apid bees, such as those in the genera *Amegilla* and *Anthophora*, are known to have greater thermoregulatory abilities and can fly in cooler temperatures than smaller bees (Linsley 1978, Herrera 1990, Stone 1994, Willmer and Stone 1997b, Stone et al. 1999b). In these studies, large bees demonstrated bimodal activity patterns, with numbers of visits peaking early in the morning and later in the afternoon when temperatures were relatively cool. At Mpala, the larger apid bees (*Amegilla*, *Anthophora*, *Tetralonia* and *Tetraloniella*) were observed visiting flowers during time periods 1 and 4, when few smaller bees were active. However, larger bees were also often observed during time periods 2 and 3. Most of these visits occurred before 11.45 and after 14.15, with only two large bee visitors observed between these times. This period was often the hottest part of the day (Fig. 6.21), and therefore these bees might have been exhibiting bimodal activity patterns that could not be detected due to the relatively broad time periods in this study.

Smaller bees were not generally active during cooler parts of the day (i.e. time periods 1 and 4). All bees were active in time periods 2 and 3, with only three of the 44 species of small to medium sized bees observed in time period 1 and eight observed in time period 4. This corresponds with predictions regarding their inability to fly during cooler temperatures (Herrera 1990, Willmer and Stone 2004).

If the activities of visitors are constrained to particular daily times, this would imply that flower-visitor interactions are structured by top-down effects. Other factors, such as daily nesting cycles, could also restrict foraging activity to particular times of day (Willmer and Stone 1989, 2004, Stone et al. 1999b). To examine the effect of pollinator behaviour on the daily timing of flower-visitor interactions, more detailed activity patterns for important pollinators in these communities are necessary. In addition to foraging activity, such studies would also need to examine bee nest sites to determine daily nesting cycles, as well as species' thermoregulatory abilities. Such comprehensive studies for a single pollinator can be labour-intensive (e.g. Stone et al. 1999b) therefore the examination of activity patterns for entire pollinator communities would be an extensive task.

### 6.4.7 Implications of this study and further work

The results of this study demonstrate that sampling of flower-visitor interactions during a limited daily time window could mean that some interactions are missed. Furthermore if interactions are grouped over daily time, then interactions among plants that share pollinators could be misinterpreted; plants that appear to be competing may not actually receive visits from shared pollinators at the same time of day.

This study also demonstrates that flowering plant communities, visitor species and their interactions vary across seasonal time, and supports the conclusion of Basilio et al. (2006) that interaction webs should not assimilate interactions over long seasonal periods if they wish to identify competitive or facilitative interactions among plant species.

What this study does not reveal is whether daily temporal patterns in plant-visitor interactions are due to the 'top-down' effects of visitor species' activity or 'bottom-up' effects dictated by the timing of pollen and nectar production of plant species. Partitioning of shared pollinators is only occurring among plant species if the timing of visits is controlled by the plants producing their rewards at a particular time in order to reduce competitive interactions.

To further investigate what might be driving the observed temporal patterns, both the bottom-up effects of plant resource provision in daily time and the top-down effects imposed by pollinators' daily activity cycles need to be investigated. Examination of the daily times of pollen release and nectar production for plant species in these communities is currently the subject of an additional study by J. C. Ruiz Guajardo (University of Edinburgh), and we hope to establish the role of resource provision in determining daily temporal structure in both communities in this study.

Further detailed observations of visitation patterns for key plant species in these communities would be useful for several reasons:

(i) to demonstrate how effective the low resolution sampling used in this study has been in demonstrating the full range of visitors and the daily visitation pattern for each plant species;

(ii) the identification of frequent visitors that could be effective pollinators for each plant species;

(iii) to more accurately investigate patterns of visitation by shared visitors on finer daily timescales.

Ideally such studies would incorporate observations of multiple plant species on the same day to minimise the effects of climatic variation between days. However the quantity of data that can be collected will inevitably be limited by the number of people available to collect it.

# Chapter 7. Conclusions and future directions

## 7.1 Results overview

At the beginning of this thesis, I set out to investigate (i) whether co-flowering acacia species at Mpala partitioned pollinator visits in daily time, (ii) whether acacias shared visitors with other plant species and (iii) the extent to which shared visitors with other flowering plant species were patterned through daily time.

In Chapter 3, I found that most acacias at Mpala had bimodal flowering phenologies with one species, *S. brevispica*, having a trimodal flowering phenology. Up to five acacia species regularly co-flowered.

In Chapter 4, I found that low intraspecific synchrony and high interspecific synchrony in the timing of dehiscence in these acacias precludes evidence for competitive displacement. Individual species found at both Mpala and the Mkomazi study site in Tanzania commonly show radically different dehiscence behaviour in terms of synchrony and structure among co-flowering species. The strong correlation between dehiscence time and relative humidity observed at Mkomazi was not demonstrated by the acacias at Mpala.

In Chapter 5, I showed that flower heads were visited mainly by bees and flies, with species falling into one of two categories: (i) those visited in similar proportions by bees and flies and (ii) those whose visits were dominated by bees. As a group, acacias shared many visitor species, in particular *Apis mellifera* and megachilid bees in the genus *Megachile*. *Megachile* dominated visits to *V. nilotica* and *Apis mellifera* dominated visits to *V. drepanolobium*, however both formed smaller proportions of overall visits to other acacias. Bees, and in some species flies, closely tracked dehiscence patterns. This suggests a bottom-up influence on plant-pollinator interactions, however there is little evidence for bottom-up structuring among co-flowering species since dehiscence patterns, and therefore visitation patterns, overlapped in daily time.

In Chapter 6, I found that acacias shared visitors with a wide range of plant species and are one of the most highly linked plants across seasonal webs. Although the composition of flower-visitor webs varied across sites and through seasons, there was consistent evidence of daily temporal structure at the web level.

Acacias show bottom-up control of visitor behaviour, particularly for bees. This means that the partitioning of pollinators would, in principle, be possible if pollen release was itself structured. A striking feature of the Mpala acacias is the absence of temporal structuring among co-flowering species. This is associated with strongly counter-intuitive relationships between relative humidity and dehiscence. So why do the acacias at Mpala behave so differently to those at Mkomazi?

## 7.2 Why is there no evidence of daily temporal structure among the acacias at Mpala?

The lack of evidence for daily temporal structuring of pollinators among co-flowering acacias at Mpala could be because:

(i) The data collected in this study do not reveal the daily temporal structure that exists among co-flowering acacias. This could be due to errors in the sampling of pollen release patterns, such as insufficient sampling, or the simultaneous sampling of different ages of flower heads. Ideally, species demonstrating complex patterns of dehiscence would be re-sampled in a more intensive fashion to rule out sampling artefacts within the current data.

(ii) The data are real (i.e. species have multiple peaks) but what we see is a result of more complicated flowering behaviour in individual trees, i.e. there might be different cohorts of flower heads with pollen available at different times of the day in species such as *S. brevispica* and *V. nilotica*. Some of the complexities in the current data could be due to an inability to separate cohorts of flower heads during sampling. Flower heads on individual *V. nilotica* trees at Mpala were sampled over consecutive days, although these data have not been presented in full in this thesis. Tracking patterns of dehiscence over several days in other species with irregular patterns of dehiscence (e.g. *S. brevispica*) could reveal the existence of more predictable patterns in daily time.

(iii) There really is no daily temporal structuring of acacia dehiscence and shared pollinators at Mpala. Even with intensive studies and the separation of different cohorts of flower heads, there might still be no regular spacing of dehiscence peaks in daily time for co-flowering acacias. This could be for several reasons:

Hypothesis 1. Shared pollinators do not contribute high enough proportions of total visits for any kind of heterospecific pollen transfer they mediate to be a problem.

Hypothesis 2. Heterospecific pollen transfer occurs but does not affect seed set.

Hypothesis 3. They are tolerant of competition because flowering seasons are longer.

Hypothesis 4. Sets of co-flowering species are unpredictable between years and between sites and therefore selection on the dehiscence time of individual acacias is not consistent. No formal analysis of seasonal flowering patterns was carried out in this thesis, although it is clear that the flowering phenologies for individual species were variable.

## 7.3 How could we determine which of these apply at Mpala?

These hypotheses could be investigated in the following ways:

*Hypothesis 1. Shared pollinators form low proportions of visits.*

Important shared pollinators for each co-flowering acacia species would need to be identified. As well as quantifying visitor frequency at the species level, evidence for pollinator efficacy could be provided by examining pollen loads. Specifically, acacias flowering at the same time in the place that will share a pool of potential pollinators should be targeted over a relatively short timescale.

*Hypothesis 2. Heterospecific pollen transfer does not affect seed set.*

Evaluation of this hypothesis would require measurement of the effect of heterospecific pollen transfer on the level of seed set for each species. This could be achieved by measuring seed set in controlled experiments in which conspecific and heterospecific pollen were artificially transferred to flower heads. Examination of this in the natural environment would be trickier, although flower heads could be examined to see what extent heterospecific pollen is transferred by pollinator visits.

This would require an ability to distinguish between pollen from different acacia species.

*Hypothesis 3. Competition is tolerated due to long flowering seasons.*

Examination of this hypothesis would require more definite proof that competition for pollinators exists among co-flowering acacias. Tolerance of competition could be shown by comparing seed set for species flowering in relative isolation from other acacias, to conspecific trees that coexist and co-flower with many species. At Mpala, this could be done most easily for *V. drepanolobium*, which dominates the woody vegetation on the black cotton soil but grows in sympatry with a wider diversity of acacias on the red soil.

*Hypothesis 4. Sets of co-flowering species are unpredictable.*

More detailed analyses of the flowering phenology data set collected at Mpala could show the regularity with which particular sets of species co-flower. Since collection of these data are ongoing a longer term data set is potentially available. In this study I had no minimum threshold flowering level for inclusion of species as co-flowering. Comparisons of the relative flowering scores would reveal the intensity with which species co-flower, and therefore indicate whether particular species in the co-flowering sets identified in this thesis are more likely to exert consistent signals on one another. It would also be interesting to know why acacia flowering patterns are so variable at Mpala in comparison to those in other locations (e.g. Stone et al. 1998, Mduma et al. 2007). More detailed analyses, including climatic factors such as rainfall, might reveal why the flowering phenologies of species at this site differ to those for the same species in other locations.

All of these hypotheses assume that competition for pollination will exist only among acacias, however the findings in Chapter 6 demonstrate that acacias are highly linked to other plant species in the community. Therefore further examinations might also include the potential for heterospecific pollen transfer from non-acacia species and consideration of their flowering phenologies.

## 7.4 Could other interaction webs be structured in daily time?

The results in Chapter 6 show that plant-visitor interactions are structured in daily time. The consideration of daily temporal variation is important for plant-pollinator communities since interactions occur over a relatively short timescale and the timing of reward presentation and pollinator activity can both be limited in daily time. The extent to which daily temporal variation is important for other types of interaction webs will depend on the timescale over which interactions occur and whether species have daily activity patterns that restrict the times at which they are available to interact.

Many animals have daily activity patterns and are active at particular times during a 24 hour period (Daan 1981 cited in Kronfeld-Schor and Dayan 2003). Climatic conditions, such as temperature and rainfall, might limit animal activity patterns (see section 6.1.1, Kowalczyk et al. 2003, Sanecki et al. 2006).

Other mutualistic relationships that have been widely studied at the community level are those between plants and their animal seed dispersers (e.g. Sorensen 1981, Wheelwright et al. 1984). Although the activity of seed dispersers might be structured in daily time, the timing of seed removal is unlikely to be important for plants. The benefit of this relationship for the plant is the actual process of dispersal, which might take place over several hours or days.

Food web studies encompass a wide diversity of communities and describe which species in a community consume which other species. Examples of interactions include those between predators and their prey (e.g. Akin and Winemiller 2006) and between parasitoids and their hosts (e.g. Lewis et al. 2002). Host-parasitoid interactions are unlikely to be structured in daily time, since interactions occur over timescales of days or weeks.

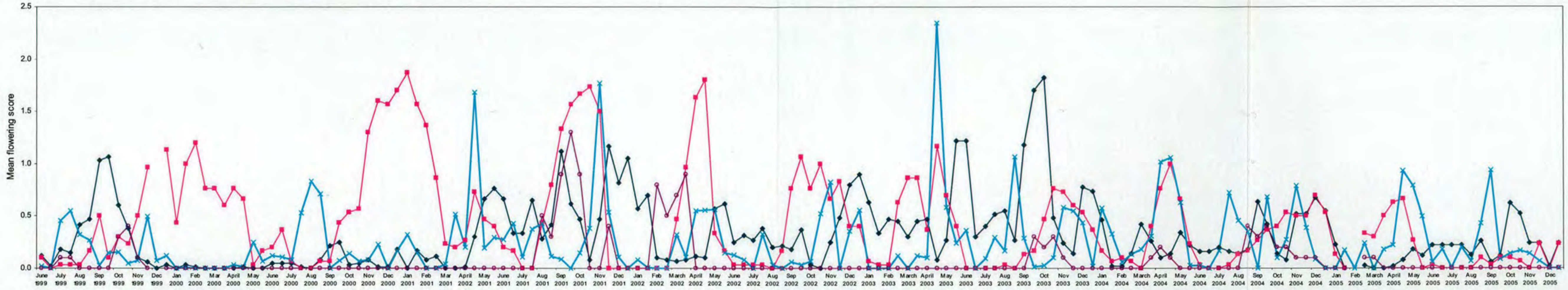
Predator-prey interactions are more likely to be structured in daily time since interactions occur over short time periods and both interacting species could have specific daily activity patterns. Prey species might limit activity to daily time periods with less risk of predation. For example, prey species might be active at night because the risk of predation is lower than during the day (e.g. Saiful et al. 2001). Predator activity and behaviour will be determined by the activity patterns of prey species. For example, if the most desirable prey species are active at night, diurnal predators could either alter their own activity patterns or consume less desirable prey species. Predators that share prey species might diverge in daily time to minimise competition. For example, it has been proposed that raptors sharing prey species reduce competition by differing in their times of daily activity, with owls active at night, and other raptors active during the day (reviewed by Jaksic 1982). This process is equivalent to pollinator partitioning in daily time among co-flowering plant species.

Given the potential for daily variation in interactions, daily temporal structure should perhaps be considered in predator-prey interaction webs. Although previous studies have considered variation in seasonal time in such webs (e.g. Schoenly and Cohen 1991, Tavares-Cromar and Williams 1996), to my knowledge none have so far incorporated variation in daily time. Consideration of webs on a daily timescale will be important if the relationships between species at the same trophic level could be misinterpreted by assimilating all interactions in one web.

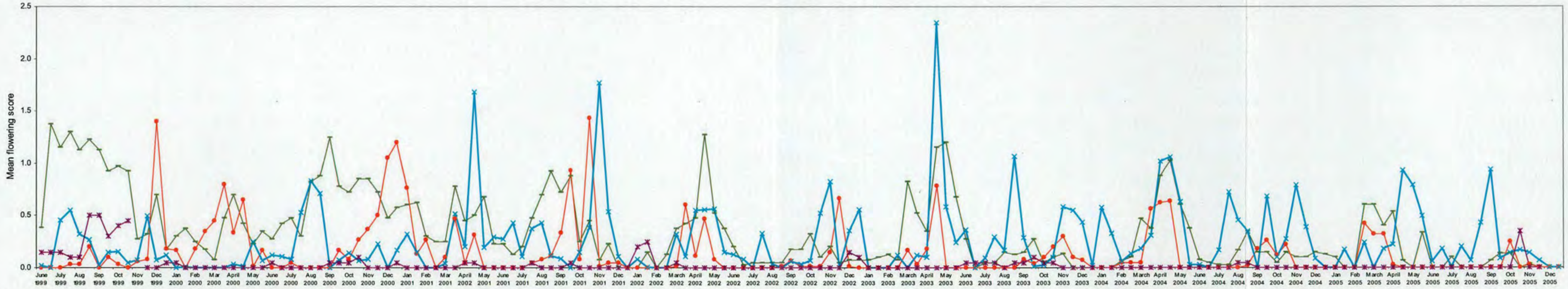
Appendix 1. Mean flowering scores for acacia species across all sites between June 1999 and December 2005. Rainfall is shown in turquoise. The rainfall scale is not shown on these graphs, however a flowering score of 1 is equivalent to 100 mm of rainfall.

Key to species:
- ◆ brevispica
- ■ drepanolobium
- ▲ etbaica
- — gerrardii
- ✶ hockii
- ● mellifera
- + nilotica
- — seyal
- ○ tortilis
- □ xanthophloea

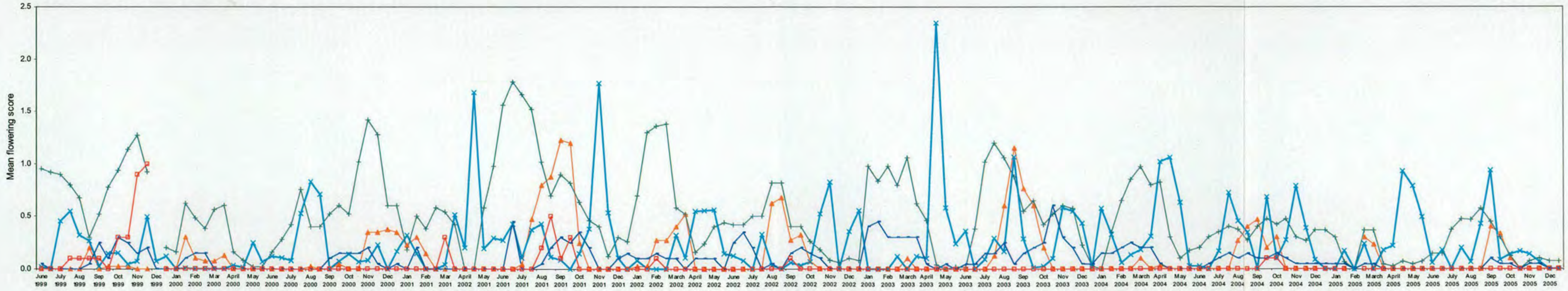
(a) *S. brevispica*, *V. drepanolobium*, *V. tortilis*



(b) *V. gerrardii*, *S. mellifera*, *V. hockii*



(c) *V. etbaica*, *V. nilotica*, *V. seyal*, *V. xanthophloea*

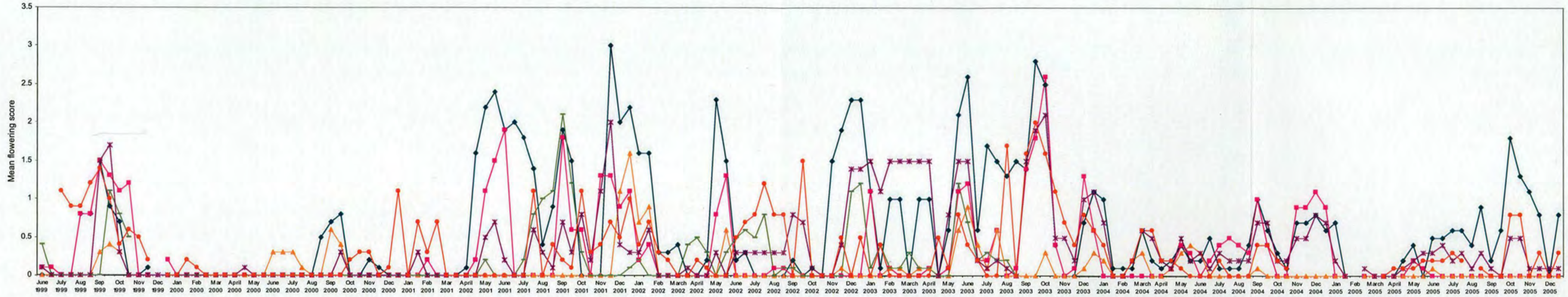


Appendix 2. Mean flowering scores for each acacia species sampled at Mpala Research Centre between June 1999 and December 2005.

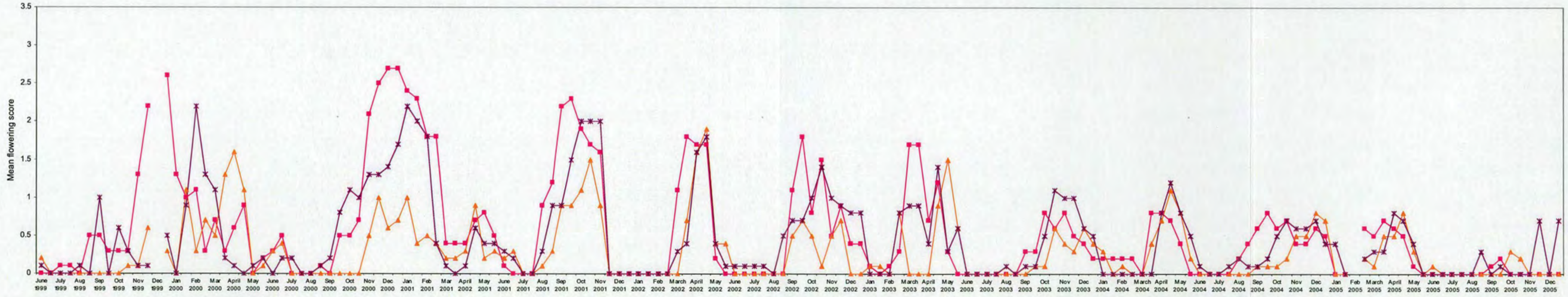
Key to sites:

- ◆ MRC
- ■ Turkana Boma
- ▲ Mongoose
- — Mukenya
- ✱ Junction
- ● High Dam

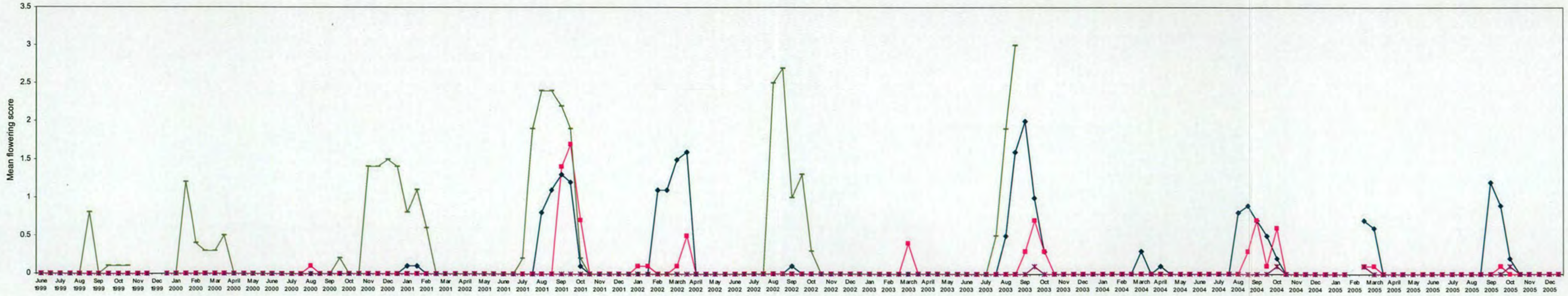
(a) *S. brevispica*



(b) *V. drepanolobium*

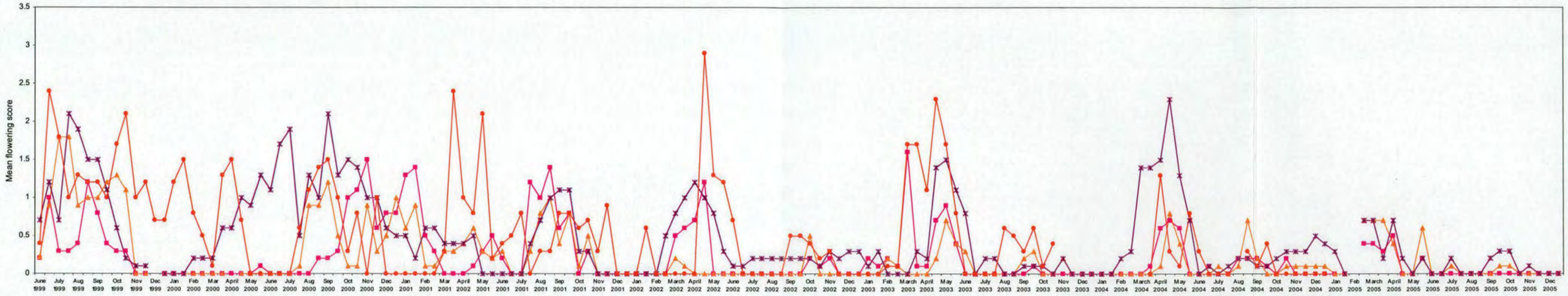


(c) *V. etbaica*

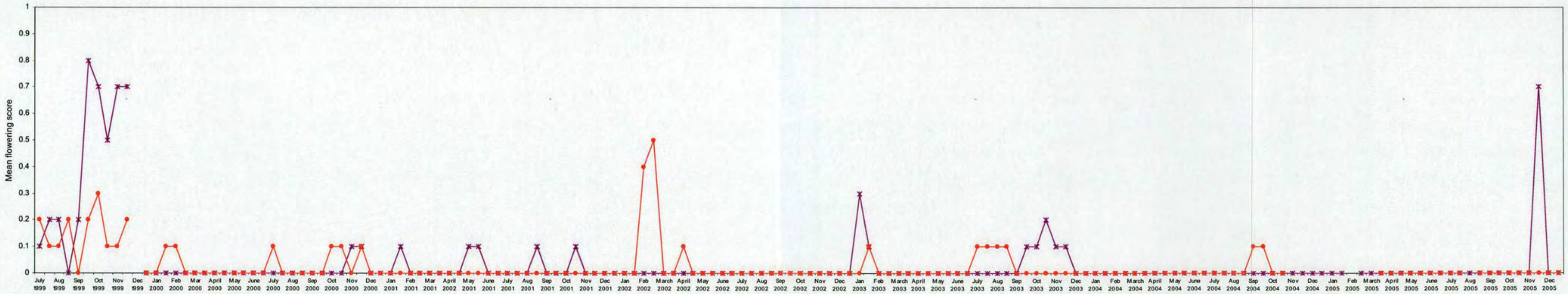


Key to sites:
- ◆ MRC
- ■ Turkana Boma
- ▲ Mongoose
- — Mukenya
- ✱ Junction
- ● High Dam

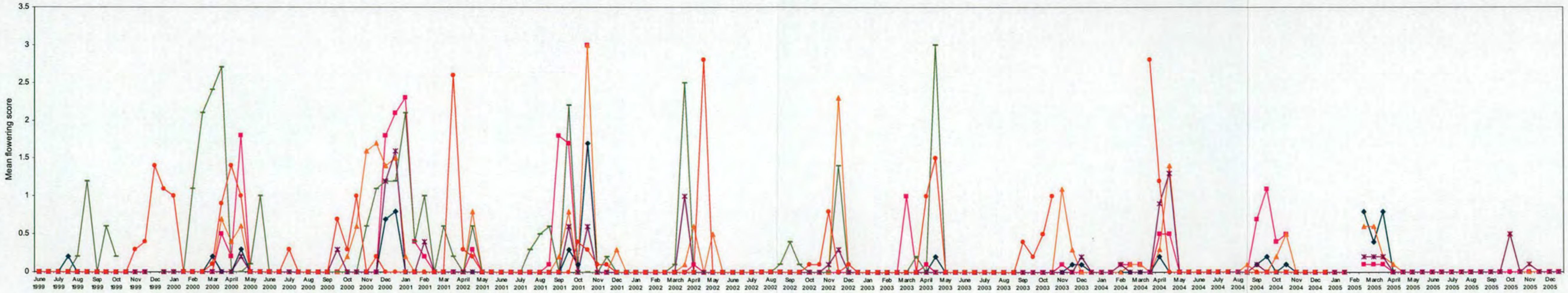
(d) *V. gerrardii*



(e) *V. hockii*



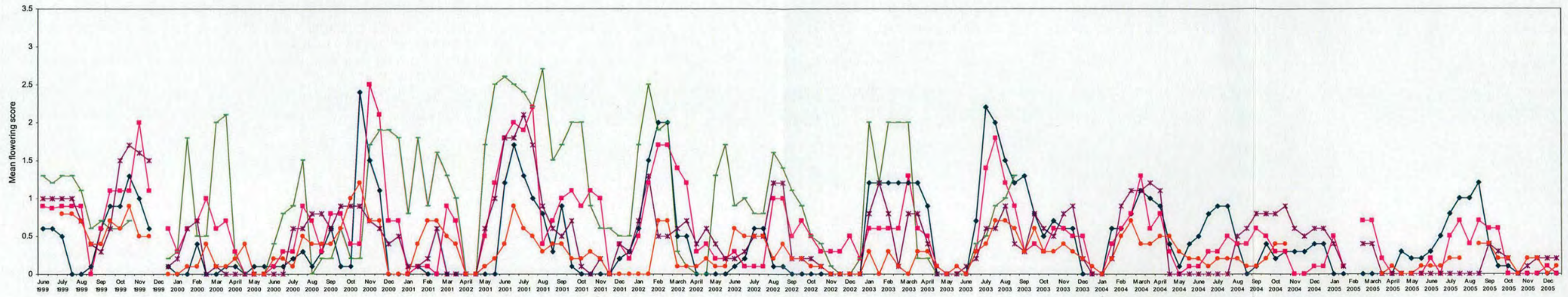
(f) *S. mellifera*



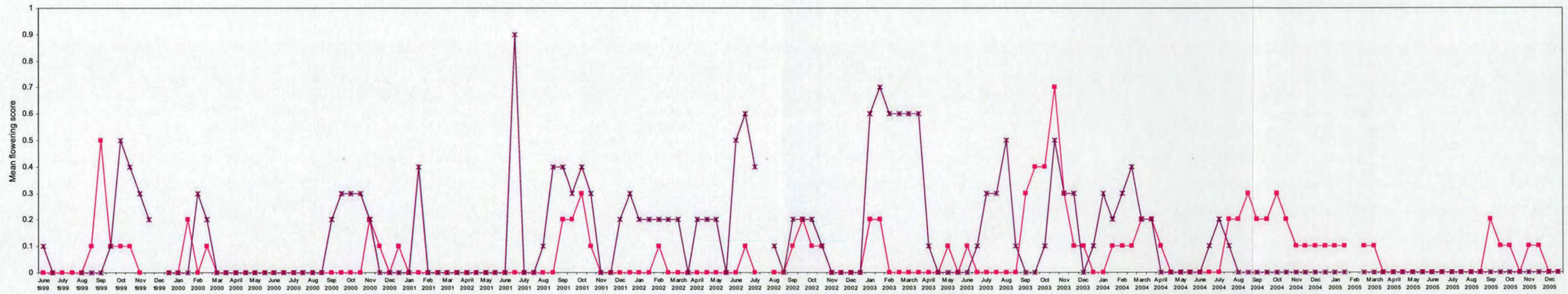
Key to sites:

- ◆ MRC
- ■ Turkana Boma
- ▲ Mongoose
- — Mukenya
- ✱ Junction
- ● High Dam

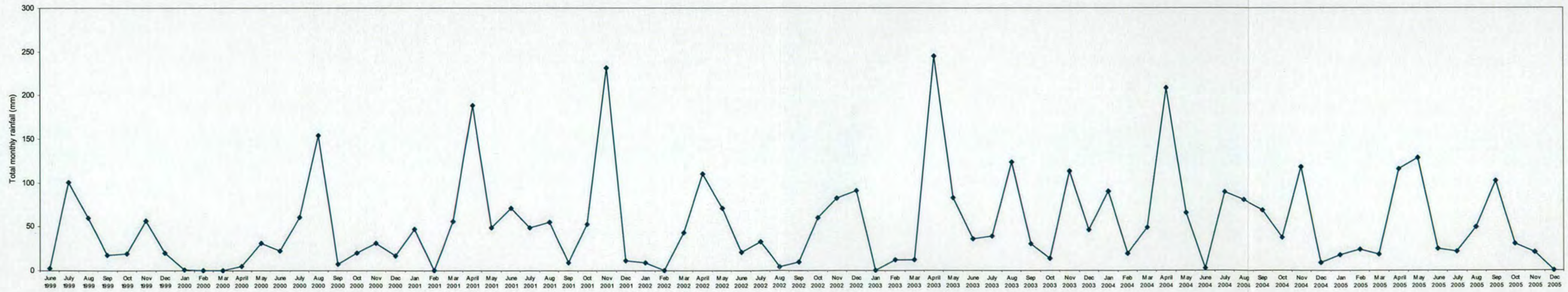
(g) *V. nilotica*



(h) *V. seyal*



Appendix 3. Total monthly rainfall near MRC site between June 1999 and December 2005.

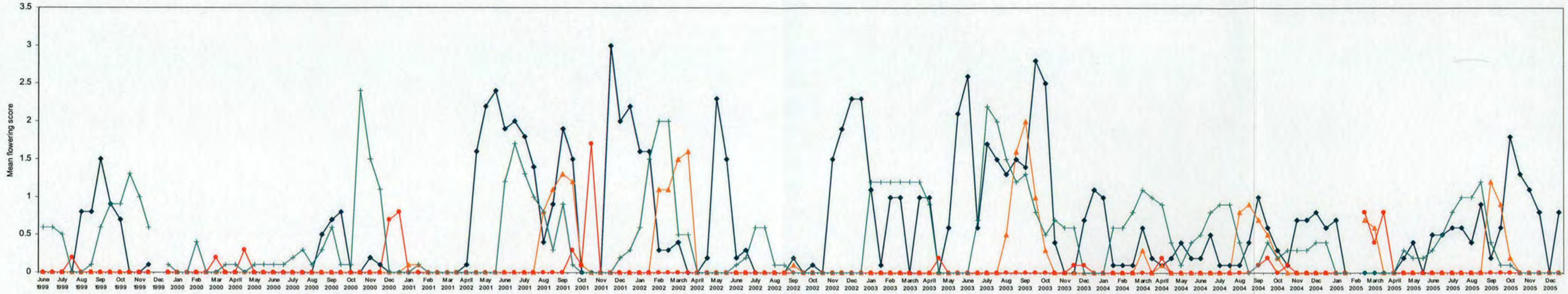


Appendix 4. Mean flowering scores for all acacia species at each site between June 1999 and December 2005.

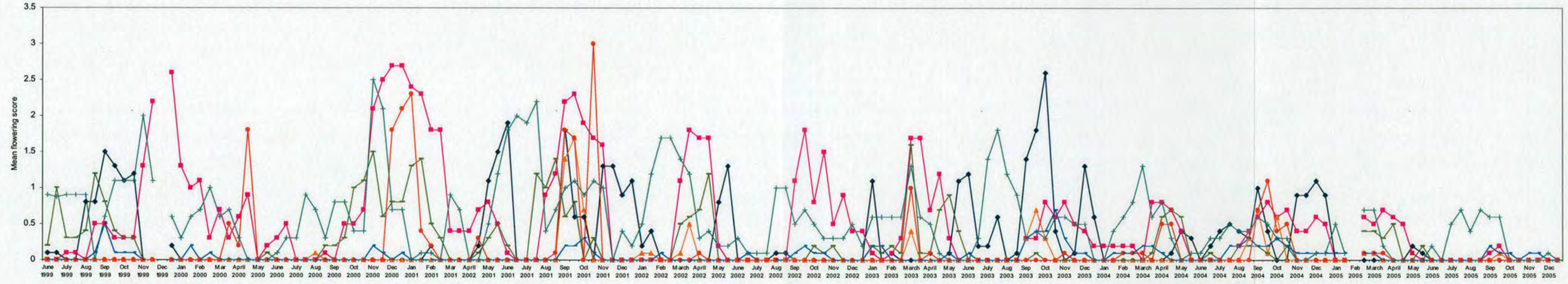
Key to species:

- ◆ brevispica
- ■ drepanolobium
- ▲ etbaica
- — gerrardii
- ✱ hockii
- ● mellifera
- + nilotica
- - seyal

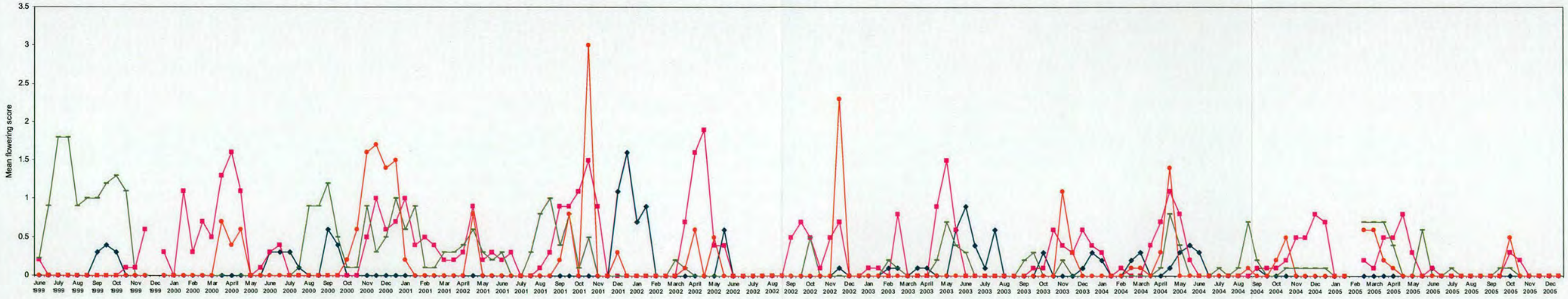
(a) Mpala



(b) Turkana Boma



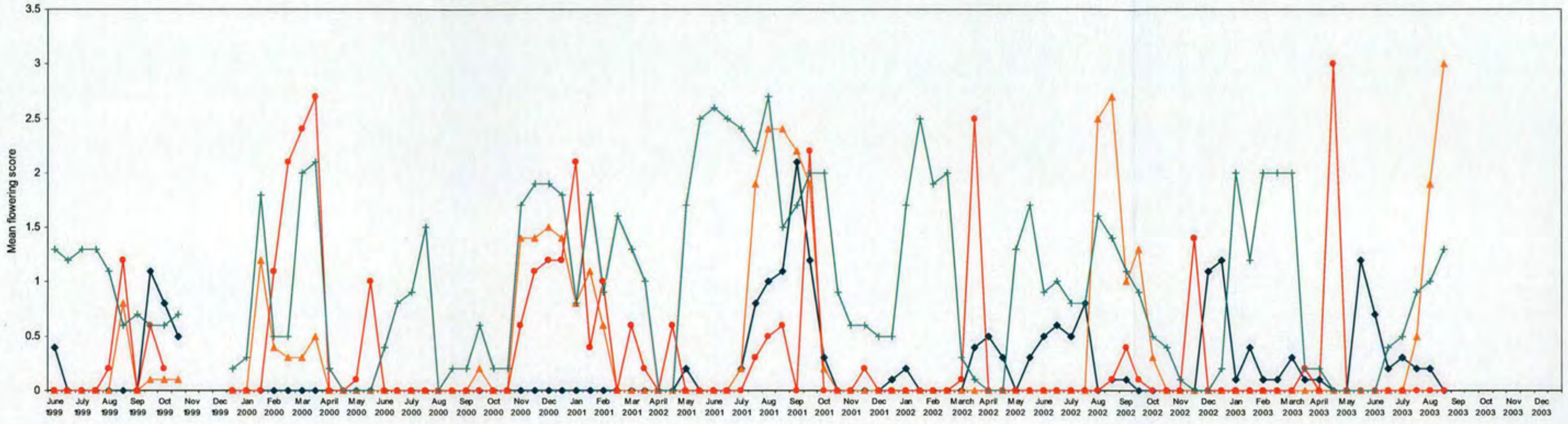
(c) Mongoose



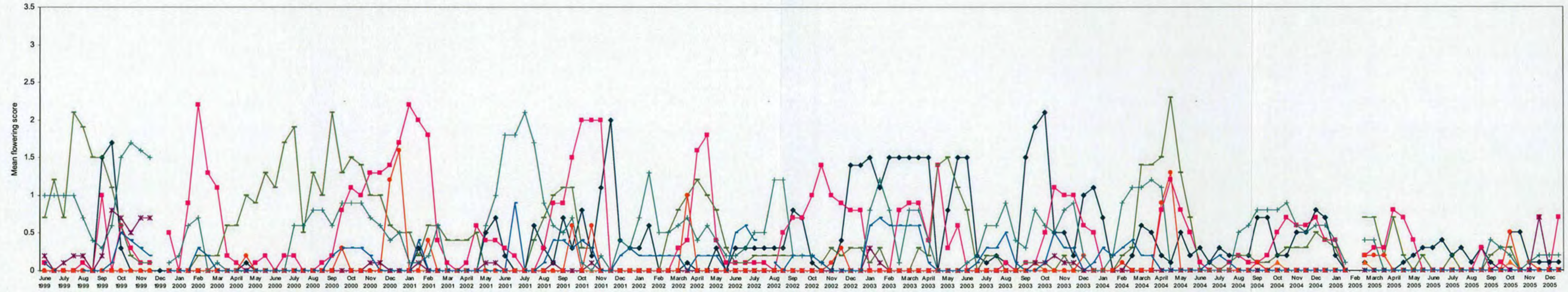
Key to species:

- ◆ brevispica
- ■ drepanolobium
- ▲ etbaica
- — gerrardii
- ✱ hockii
- ● mellifera
- \+ nilotica
- \- seyal

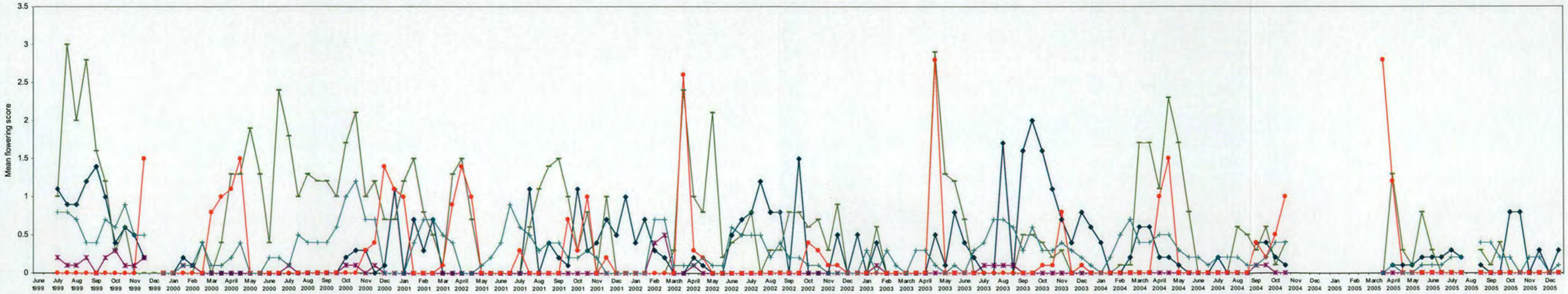
(d) Mukenya



(e) Junction



(f) High Dam



Appendix 5. The frequency with which groups of acacia species at each site co-flower. The number of sampling points for which species flowered at a particular site is given underneath the species name. The number of sampling points and the percentage of total sampling points for which groups of species co-flowered are shown. b: *S. brevispica*, d: *V. drepanolobium*, e: *V. etbaica*, g: *V. gerrardii*, h: *V. hockii*, m: *S. mellifera*, n: *V. nilotica*, s: *V. seyal*.

(a) Mpala

Total 156 sampling points, *S. brevispica*: 102, *V. etbaica*: 29, *S. mellifera*: 18, *V. nilotica*: 103

| **Species combinations** | **No. sampling points** | **% sampling points** |
|---|---|---|
| **2 species** | | |
| bn | 73 | 47 |
| be | 25 | 16 |
| en | 23 | 15 |
| em | 6 | 4 |
| bm | 4 | 3 |
| mn | 4 | 3 |
| **3 species** | | |
| ben | 21 | 13 |
| bem | 3 | 2 |
| bmn | 3 | 2 |
| emn | 3 | 2 |
| **4 species** | | |
| bemn | 3 | 2 |

(b) Turkana Boma

Total 156 sampling points, *S. brevispica*: 60, *V. drepanolobium*: 102, *V. etbaica*: 19, *V. gerrardii*: 67, *S. mellifera*: 29, *V. nilotica*: 129, *V. seyal*: 57

| **Species combinations** | **No. sampling points** | **% sampling points** |
|---|---|---|
| **2 species** | | |
| dn | 85 | 54 |
| dg | 58 | 37 |
| gn | 57 | 37 |
| ns | 49 | 31 |
| bn | 46 | 29 |
| ds | 46 | 29 |
| bd | 37 | 24 |
| bg | 29 | 19 |
| dm | 28 | 18 |
| bs | 26 | 17 |
| gs | 26 | 17 |
| mn | 26 | 17 |
| gm | 21 | 13 |
| en | 19 | 12 |
| de | 16 | 10 |
| ms | 15 | 10 |
| es | 13 | 8 |

| Species combinations | No. sampling points | % sampling points |
|---|---|---|
| be | 11 | 7 |
| eg | 11 | 7 |
| bm | 8 | 5 |
| em | 8 | 5 |
| **3 species** | | |
| dgn | 49 | 31 |
| dns | 37 | 24 |
| bdg | 28 | 18 |
| dgm | 26 | 17 |
| bdn | 25 | 16 |
| gns | 25 | 16 |
| dgs | 25 | 16 |
| dmn | 24 | 15 |
| bgn | 22 | 14 |
| bds | 19 | 12 |
| gmn | 18 | 12 |
| bns | 16 | 10 |
| den | 16 | 10 |
| mns | 15 | 10 |
| bgs | 14 | 9 |
| dms | 14 | 9 |
| des | 13 | 8 |
| ens | 13 | 8 |
| ben | 11 | 7 |
| deg | 11 | 7 |
| egn | 11 | 7 |
| egs | 10 | 6 |
| gms | 10 | 6 |
| bde | 9 | 6 |
| bdm | 9 | 6 |
| bes | 9 | 6 |
| bgm | 9 | 6 |
| dem | 8 | 5 |
| emn | 8 | 5 |
| egm | 7 | 4 |
| ems | 7 | 4 |
| bmn | 7 | 4 |
| beg | 6 | 4 |
| **4 species** | | |
| dgns | 24 | 15 |
| bdgn | 19 | 12 |
| dgmn | 19 | 12 |
| bdns | 15 | 10 |
| bdgs | 14 | 9 |
| dmns | 14 | 9 |
| dens | 13 | 8 |
| bgns | 12 | 8 |
| degn | 11 | 7 |

| Species combinations | No. sampling points | % sampling points |
|---|---|---|
| degs | 10 | 6 |
| dgms | 10 | 6 |
| gmns | 10 | 6 |
| bdgm | 9 | 6 |
| bden | 9 | 6 |
| bdes | 9 | 6 |
| bens | 9 | 6 |
| demn | 8 | 5 |
| egns | 8 | 5 |
| degm | 7 | 4 |
| dems | 7 | 4 |
| egmn | 7 | 4 |
| emns | 7 | 4 |
| bdeg | 6 | 4 |
| begn | 6 | 4 |
| begs | 6 | 4 |
| egms | 6 | 4 |
| bdmn | 3 | 2 |
| bgmn | 3 | 2 |
| **5 species** | | |
| bdgns | 12 | 8 |
| dgmns | 10 | 6 |
| bdens | 9 | 6 |
| degns | 8 | 5 |
| degmn | 7 | 5 |
| demns | 7 | 5 |
| bdegn | 6 | 4 |
| bdegs | 6 | 4 |
| begns | 6 | 4 |
| degms | 6 | 4 |
| egmns | 6 | 4 |
| bdgmn | 3 | 2 |
| **6 species** | | |
| bdegns | 6 | 4 |
| degmns | 6 | 4 |
| **7 species** | | |
| bdegmns | 4 | 3 |

(c) Mongoose

Total 156 sampling points, *S. brevispica*: 36, *V. drepanolobium*: 87, *V. gerrardii*: 72, *S. mellifera*: 33

| Species combinations | No. sampling points | % sampling points |
|---|---|---|
| **2 species** | | |
| dg | 45 | 29 |
| dm | 27 | 17 |
| gm | 22 | 14 |
| bd | 12 | 8 |
| bg | 11 | 7 |
| bm | 2 | 1 |
| **3 species** | | |
| dgm | 16 | 10 |
| bdg | 3 | 2 |
| bdm | 1 | 1 |
| bgm | 1 | 1 |
| **4 species** | | |
| bdgm | 1 | 1 |

(d) Mukenya

Total 101 sampling points, *S. brevispica*: 41, *V. etbaica*: 34, *S. mellifera*: 36, *V. nilotica*: 87

| Species combinations | No. sampling points | % sampling points |
|---|---|---|
| **2 species** | | |
| bn | 30 | 30 |
| en | 30 | 30 |
| mn | 26 | 26 |
| em | 21 | 21 |
| be | 12 | 12 |
| bm | 10 | 10 |
| **3 species** | | |
| emn | 20 | 20 |
| ben | 14 | 14 |
| bmn | 10 | 10 |
| bem | 8 | 8 |
| **4 species** | | |
| bemn | 8 | 8 |

(e) Junction
Total 156 sampling points, *S. brevispica*: 99, *V. drepanolobium*: 107, *V. etbaica*: 4, *V. gerrardii*: 116, *V. hockii*: 25, *S. mellifera*: 20, *V. nilotica*: 114, *V. seyal*: 65

| **Species combinations** | **No. sampling points** | **% sampling points** |
|---|---|---|
| **2 species** | | |
| gn | 86 | 55 |
| dg | 81 | 52 |
| dn | 80 | 51 |
| bn | 71 | 46 |
| bd | 67 | 43 |
| bg | 67 | 43 |
| ns | 58 | 37 |
| bs | 49 | 31 |
| gs | 47 | 30 |
| ds | 43 | 28 |
| hn | 24 | 15 |
| gh | 22 | 14 |
| dh | 20 | 13 |
| gm | 19 | 12 |
| hs | 17 | 11 |
| dm | 16 | 10 |
| bh | 15 | 10 |
| bm | 13 | 8 |
| mn | 13 | 8 |
| eg | 4 | 3 |
| en | 4 | 3 |
| ms | 4 | 3 |
| be | 3 | 2 |
| de | 3 | 2 |
| em | 2 | 1 |
| eh | 1 | 1 |
| hm | 1 | 1 |
| hm | 1 | 1 |
| es | 0 | 0 |
| **3 species** | | |
| dgn | 64 | 41 |
| bdn | 51 | 33 |
| bgn | 51 | |
| bdg | 49 | 33 |
| gns | 43 | 31 |
| dns | 39 | 28 |
| dgs | 35 | 25 |
| bgs | 32 | 22 |
| bns | 31 | 20 |
| bds | 29 | 19 |
| ghn | 20 | 13 |
| dhn | 18 | 12 |
| bhn | 16 | 10 |

| Species combinations | No. sampling points | % sampling points |
|---|---|---|
| dgm | 15 | 10 |
| dgh | 15 | 10 |
| hns | 15 | 10 |
| bdh | 14 | 9 |
| ghs | 14 | 9 |
| gmn | 13 | 8 |
| dhs | 13 | 8 |
| bgm | 12 | 7 |
| bhs | 12 | 7 |
| bgh | 11 | 7 |
| dmn | 11 | 7 |
| bdm | 10 | 6 |
| bmn | 9 | 6 |
| egn | 4 | 3 |
| bde | 4 | 3 |
| beg | 4 | 3 |
| ben | 4 | 3 |
| gms | 4 | 3 |
| bms | 3 | 2 |
| deg | 3 | 2 |
| den | 3 | 2 |
| dms | 3 | 2 |
| mns | 3 | 2 |
| bem | 2 | 1 |
| egm | 2 | 1 |
| emn | 2 | 1 |
| beh | 1 | 1 |
| bhm | 1 | 1 |
| deh | 1 | 1 |
| dem | 1 | 1 |
| dhm | 1 | 1 |
| egh | 1 | 1 |
| ehn | 1 | 1 |
| ghm | 1 | 1 |
| hms | 1 | 1 |
| **4 species** | | |
| bdgn | 39 | 25 |
| dgns | 31 | 20 |
| bgns | 28 | 18 |
| bdns | 25 | 16 |
| bdgs | 22 | 14 |
| dghn | 14 | 9 |
| dghs | 14 | 9 |
| bdhn | 13 | 8 |
| ghns | 13 | 8 |
| dhns | 12 | 8 |
| bghn | 11 | 7 |
| dgmn | 10 | 6 |

| Species combinations | No. sampling points | % sampling points |
|---|---|---|
| bghs | 10 | 6 |
| bdgm | 9 | 6 |
| bdgh | 9 | 6 |
| bdhs | 9 | 6 |
| bhns | 9 | 6 |
| bgmn | 8 | 5 |
| bdmn | 7 | 4 |
| begn | 4 | 3 |
| gmns | 3 | 2 |
| bdeg | 3 | 2 |
| bden | 3 | 2 |
| bdms | 3 | 2 |
| bgms | 3 | 2 |
| degn | 3 | 2 |
| dgms | 3 | 2 |
| begm | 2 | 1 |
| bemn | 2 | 1 |
| bmns | 2 | 1 |
| dmns | 2 | 1 |
| egmn | 1 | 1 |
| bdeh | 1 | 1 |
| bdem | 1 | 1 |
| bdhm | 1 | 1 |
| begh | 1 | 1 |
| behn | 1 | 1 |
| bghm | 1 | 1 |
| bhms | 1 | 1 |
| degh | 1 | 1 |
| degm | 1 | 1 |
| dehn | 1 | 1 |
| demn | 1 | 1 |
| dghm | 1 | 1 |
| dhms | 1 | 1 |
| eghn | 1 | 1 |
| ghms | 1 | 1 |
| **5 species** | | |
| bdgns | 20 | 13 |
| dghns | 9 | 6 |
| bghns | 9 | 6 |
| bdgns | 8 | 5 |
| bdhns | 8 | 5 |
| bdghn | 8 | 5 |
| bdghs | 7 | 4 |
| bdgmn | 6 | 4 |
| bdgms | 3 | 2 |
| bdegn | 3 | 2 |
| begmn | 2 | 1 |
| bdmns | 2 | 1 |

| Species combinations | No. sampling points | % sampling points |
|---|---|---|
| bdegh | 1 | 1 |
| bdegm | 1 | 1 |
| bdehn | 1 | 1 |
| bdemn | 1 | 1 |
| bdghm | 1 | 1 |
| bdhms | 1 | 1 |
| beghn | 1 | 1 |
| bghms | 1 | 1 |
| degmn | 1 | 1 |
| deghn | 1 | 1 |
| dghms | 1 | 1 |
| **6 species** | | |
| bdghns | 6 | 4 |
| bdgmns | 2 | 1 |
| bdghms | 1 | 1 |
| bdegmn | 1 | 1 |
| bdeghn | 1 | 1 |

(f) High Dam

Total 145 sampling points, *S. brevispica*: 85, *V. gerrardii*: 93, *V. hockii*: 25, *S. mellifera*: 39, *V. nilotica*: 117

| Species combinations | No. sampling points | % sampling points |
|---|---|---|
| **2 species** | | |
| gn | 88 | 60 |
| bn | 66 | 46 |
| bg | 55 | 38 |
| gm | 33 | 23 |
| mn | 29 | 20 |
| hn | 24 | 17 |
| bh | 20 | 14 |
| bm | 19 | 13 |
| gh | 15 | 10 |
| hm | 4 | 3 |
| **3 species** | | |
| bgn | 49 | 34 |
| gmn | 26 | 18 |
| bgm | 19 | 13 |
| bhn | 19 | 13 |
| bmn | 18 | 12 |
| ghn | 14 | 10 |
| bgh | 13 | 9 |
| ghm | 4 | 3 |
| hmn | 4 | 3 |
| **4 species** | | |
| bgmn | 16 | 11 |
| bghn | 10 | 7 |
| bhmn | 4 | 3 |
| ghmn | 4 | 3 |
| bghm | 3 | 2 |
| **5 species** | | |
| bghmn | 3 | 2 |

Appendix 6. Identified visitor species caught on acacia flower heads between 2003 and 2005. brev: *S. brevispica*, drep: *V. drepanolobium*, etb: *V. etbaica*, mell: *S. mellifera*, nilo: *V. nilotica*.

(a) Bees

| | **brev** | **drep** | **etb** | **gerr** | **mell** | **nilo** | **No. species caught on** |
|---|---|---|---|---|---|---|---|
| **Apidae** | | | | | | | |
| *Amegilla rapida* (Smith) | | | | | * | | 1 |
| *Amegilla penicula* Eardley & Brooks | | | | | * | | 1 |
| *Amegilla calens* (Lepeletier) | | | | | * | | 1 |
| *Anthophora pygmaea* Meade-Waldo | | | | | | * | 1 |
| *Tetraloniella alboscopacea* (Friese) | | | | | | * | 1 |
| *Apis mellifera* L. | * | * | * | * | * | * | 6 |
| *Braunsapis ?bouyssoui* (Vachal) | * | * | * | * | * | * | 6 |
| *Ceratina lunata* Friese | * | | | | | | 1 |
| *Ceratina moerenhouti* (Vachal) | | * | * | | * | * | 4 |
| *Macrogalea candida* (Smith) | * | * | * | * | * | * | 6 |
| *Plebeina hildebranti* (Friese) | * | * | * | | * | * | 5 |
| *Xylocopa somalica* Magretti | | | | | * | * | 2 |
| *Thyreus calceatus* (Vachal) | | | | | | * | 1 |
| **Colletidae** | | | | | | | |
| *Colletes* sp. 1 | * | * | | * | | | 3 |
| *Colletes* sp. 2 | | | * | | | | 1 |
| *Colletes* sp. 4 | | | * | | | * | 2 |
| *Hylaeus* sp. 1 | | * | | * | | | 2 |
| *Hylaeus* sp. 2 | | * | | | | | 1 |
| *Hylaeus* sp. 3 | | * | | | | | 1 |
| *Hylaeus* sp. 4 | * | | | * | | * | 3 |
| *Hylaeus* sp. 5 | * | | | | * | * | 3 |
| **Halictidae** | | | | | | | |
| *Halictus* (*Seladonia*) sp. 1 | | * | | * | | | 2 |
| *Halictus* (*Seladonia*) sp. 2 | | * | | | | | 1 |
| *Halictus* (*Seladonia*) sp. A | | | * | | | | 1 |
| *Halictus* (*Seladonia*) sp. B | | | | * | | | 1 |
| *Halictus* (*Seladonia*) sp. C | | * | * | * | | * | 3 |
| *Lasioglossum* (*Dialictus*) sp. 2 | | | * | | * | | 2 |
| *Lasioglossum* sp. B | | | | | * | | 1 |
| *Lasioglossum* sp. C | | * | | | * | * | 3 |
| *Lipotriches* (*Lipotriches*) sp. 1 | | | * | | | | 1 |
| *Lipotriches* (*Lipotriches*) sp. A | | * | | | | | 1 |
| *Lipotriches* (*Lipotriches*) sp. J | | | | * | | | 1 |
| *Nomia* (*Nomia*) sp. 1 | * | * | | | | | 2 |
| *Nomia* (*Nomia*) sp. 2 | | | | * | | | 1 |
| *Nomia* (*Leuconomia*) sp. 1 | | * | | | | | 1 |
| *Nomia* sp. A | | | | | * | | 1 |
| *Patellapis* (*Zonalictus*) sp. 1 | * | | | | | | 1 |
| *Patellapis* sp. B | | | | | * | | 1 |
| *Pseudapis* (*Pseudapis*) sp. 1 | * | * | * | * | * | * | 6 |

| | brev | drep | etb | gerr | mell | nilo | No. species caught on |
|---|---|---|---|---|---|---|---|
| **Megachilidae** | | | | | | | |
| *Coelioxys* (*Coelioxys*) sp. 1 | * | | | | | | 1 |
| *Megachile discolor* Smith | | * | | | * | * | 3 |
| *Megachile* (*Chalicodoma*) sp. 1 | * | * | * | | * | * | 5 |
| *Megachile* (*Chalicodoma*) sp. 2 | * | * | | * | * | * | 5 |
| *Megachile* (*Chalicodoma*) sp. 3 | | * | | * | | | 2 |
| *Megachile* (*Chalicodoma*) sp. 5 | | | | | * | | 1 |
| *Megachile* (*Paracella*) sp. 1 | * | | | | | | 1 |
| *Megachile* (*Pseudomegachile*) sp. 1 | | | | | * | | 1 |
| Osmiini sp. b | | | * | | * | | 2 |
| Osmiini sp. d | | * | | | * | | 2 |
| Osmiini sp. f | | | | * | | | 1 |
| Osmiini sp. j | | | | * | * | | 2 |
| **Melittidae** | | | | | | | |
| *Melitta katherinae* Eardley | | | | * | | | 1 |

(b) Wasps

| | brev | drep | etb | gerr | mell | nilo | No. species caught on |
|---|---|---|---|---|---|---|---|
| **Agaonidae** | | | | | | | |
| Agaonidae sp. 1 | | | * | | | | 1 |
| **Braconidae** | | | | | | | |
| *Iphiaulax* ?nr. *coccineus* | * | | | | | | 1 |
| **Chalcidae** | | | | | | | |
| Chalcididae gen. sp. indet. | | | | * | | | 1 |
| **Chrysididae** | | | | | | | |
| Chrysididae spp. | * | | * | | | | 2 |
| **Eumenidae** | | | | | | | |
| *Delta* sp. 1 | | | * | | * | | 2 |
| *Delta* sp. 2 | * | | * | | * | | 3 |
| *Delta lepeleterii* | * | | | | * | | 2 |
| *Delta ?hottentottum* | * | | * | | | * | 3 |
| *Delta emarginatum fenestralis* | | | | | * | | 1 |
| Eumenidae sp. 3 | * | * | | | | * | 3 |
| Eumenidae sp. 4 | * | * | | * | * | | 4 |
| Eumenidae sp. 5 | * | | * | | | | 2 |
| Eumenidae sp. 6 | | * | | | | | 1 |
| Eumenidae sp. 7 | | | | * | | | 1 |
| Eumenidae sp. 9 | | | * | * | | | 2 |
| Eumenidae sp. 11 | | * | | | | | 1 |
| Eumenidae sp. 14 | | | * | * | | | 2 |
| Eumenidae sp. 15 | | * | * | | * | | 3 |
| Eumenidae spp. unknown | * | * | | | | | 2 |
| **Ichneumonidae** | | | | | | | |
| Ichneumonidae spp. unknown | | * | | | | | 1 |
| *Syzeuctus* sp. 1 | | | | | * | | 1 |

| | brev | drep | etb | gerr | mell | nilo | No. species caught on |
|---|---|---|---|---|---|---|---|
| **Pompilidae** | | | | | | | |
| Pompilidae sp. 1 | * | | | | | | 1 |
| Pompilidae sp. 3 | | | | | | * | 1 |
| Pompilidae sp. 7 | | | | | * | | 1 |
| Pompilidae sp. 8 | * | | | | | | 1 |
| Pompilidae sp. 12 | | * | | | | | 1 |
| Pompilidae sp. 14 | | * | | | | | 1 |
| **Scoliidae** | | | | | | | |
| ?*Cathimeris clotho* | * | | | | | | 1 |
| *Cathimeris* ?*socotrana* Kirby | | | | | * | | 1 |
| *Scolia masiensis* Bradley | | * | | | | | 1 |
| Scoliidae sp. 1 | * | * | | | | | 2 |
| **Sphecidae** | | | | | | | |
| *Ammophila* sp. 1 | * | * | | | | * | 3 |
| *Bembix* ?*forcipata* | * | | * | * | | * | 4 |
| *Bembix* sp. 4 | | | * | | | | 1 |
| *Cerceris* sp. 1 | * | * | * | * | | * | 5 |
| *Cerceris* sp. 2 | * | * | * | | * | * | 5 |
| *Cerceris* sp. 3 | | | | | * | | 1 |
| *Dasyproctus* sp. 1 | | * | | | | | 1 |
| *Oxybelus* spp. | * | * | | * | | | 3 |
| *Philanthus* sp. 1 | * | * | * | | * | | 4 |
| *Philanthus* sp. 3 | | * | | | | | 1 |
| *Sceliphron* sp. 1 | * | | | | | | 1 |
| *Sphex* sp. 1 | * | | * | * | * | | 4 |
| *Sphex* sp. 2 | * | | | * | * | | 3 |
| *Sphex* sp. 3 | * | | | | * | * | 3 |
| *Tachytes* sp. 1 | * | | | | | | 1 |
| *Liris* sp. 1 | | | | * | | | 1 |
| Larrinae spp. unknown | | | | * | | | 1 |
| **Tiphiidae** | | | | | | | |
| Tiphiidae sp. 1 | | | * | * | | | 2 |
| Tiphiidae sp. 2 | * | | | | | | 1 |
| **Vespidae** | | | | | | | |
| *Belanogaster* sp. 1 | * | | * | | | | 2 |
| ?*Polistes* spp. | * | | | | | | 1 |

(c) Diptera (flies)

| | brev | drep | etb | gerr | mell | nilo | No. species caught on |
|---|---|---|---|---|---|---|---|
| **Asilidae** | | | | | | | |
| *Laxenecera* sp. 1 | * | | | | | * | 2 |
| *Gonioscelis* sp. 1 | | | | | | * | 1 |
| *Neolophonotus* sp. 1 | | | | | | * | 1 |
| **Bombyliidae** | | | | | | | |
| *Bombylella delicata* (Wiedemann) | * | | | | * | | 2 |
| *Bombylella auricoma* (Bezzi) | * | | | | | | 1 |
| *Bombylius acrophylax* (Greathead) | * | | | | | * | 2 |
| *Exhyalanthrax flammiger* Walker | * | | | | * | | 2 |
| *Exoprosopa* n. sp. nr. *serva* Bezzi | | * | | * | | | 2 |
| *Heteralonia katonae* (Bezzi) | * | | | * | | | 2 |
| *Systoechus cellularis* Bowden | | | | | * | | 1 |
| *Villa paniscoides* Bezzi | | * | | | | | 1 |
| **Calliphoridae** | | | | | | | |
| ?*Stomorhina* sp. | * | | | | | | 1 |
| *Chrysomya chloropyga* (Wiedemann) | * | | * | | * | * | 4 |
| *Chrysomya regalis* Robineau-Desvoidy | * | | * | | | | 2 |
| *Hemipyrellia fernandica* (Macquart) | * | * | | | | * | 3 |
| *Isomyia tristis* (Bigot) | * | | | * | | * | 3 |
| *Lucilia cuprina* Wiedemann | | * | | | | | 1 |
| *Lucilia sericata* (Meigen) | | | * | | | | 1 |
| *Pararhyncomya cribiformis* Becker | | * | * | * | | | 3 |
| *Rhinia* spp. unknown | * | | * | | | | 2 |
| *Rhinia* ?*apicalis* (Wiedemann) | * | | | | | | 1 |
| *Rhyncomya cassotis* (Walker) | | | * | | | | 1 |
| *Rhyncomya forcipata* Villeneuve | | * | * | * | * | * | 5 |
| *Rhyncomya soyauxi* Karsch | | * | * | | | * | 3 |
| *Rhyncomya trispina* Villeneuve | | | | | | * | 1 |
| *Rhyncomya* ?*tristis* Seguy | | | * | | | | 1 |
| *Rhyncomya* unknown | * | * | * | | * | | 4 |
| **Lonchaeidae** | | | | | | | |
| Lonchaeidae sp. | | | * | | | | 1 |
| **Muscidae** | | | | | | | |
| *Mitroplatia pyrellioides* Curran | | | * | | | | 1 |
| *Mitroplatia smaragdina* Seguy | * | | | | | | 1 |
| *Curranosia spekei* Jaennicke | * | | * | | | | 2 |
| *Helina coniformis* Stein | | | | * | | | 1 |
| *Musca aethiops* (Stein) | * | | * | | | | 2 |
| *Musca calleva* L. | * | | | | | | 1 |
| *Coenosia simulans* Paterson | | | | | | * | 1 |
| *Coenosia cuthbertsoni* Curran | | | | | | * | 1 |
| *Musca conducens* Walker | | | | * | | | 1 |
| *Musca domestica calleva* Walker | | | | | * | | 1 |
| *Musca domestica curviforceps* Sacca & Rivosecchi | | | * | | | | 1 |
| *Musca lusoria* Wiedemann | * | * | * | | * | * | 5 |
| *Musca* sp. nr. *lusoria* Wiedemann | | | * | | | | 1 |

| | brev | drep | etb | gerr | mell | nilo | No. species caught on |
|---|---|---|---|---|---|---|---|
| *Musca munroi* Patton | | | | | | * | 1 |
| *Musca nevilli* Kleynhans | | | * | | | | 1 |
| *Musca sorbens* Wiedemann | | | * | | | | 1 |
| *Musca alpesa* Walker | | | * | | | | 1 |
| *Musca biseta* Hough | * | | | | | | 1 |
| *Musca xanthomelaena* Wiedemann | | | * | | | * | 2 |
| *Pyrellia* sp. nov. *** | * | | * | * | | * | 4 |
| **Sarcophagidae** | | | | | | | |
| *Hilarella* sp. | | * | | | | * | 2 |
| *Hoplacephala inermis* Villeneuve | * | * | | | | | 2 |
| *Metapodiella* sp. | | * | | | | | 1 |
| *Metopia* sp. nr. *benoiti* Zumpt | | | | * | | | 1 |
| *Pterella* sp. | | | | | * | | 1 |
| **Syrphidae** | | | | | | | |
| *Allobacha sapphirina* Wiedemann | | | | * | * | | 2 |
| *Allograpta nasuta* (Macquart) | | | * | | | | 1 |
| *Ceriana caffra* (Loew) | * | * | | * | | * | 4 |
| *Eristalinus barclayi* (Bezzi) | * | | | | | | 1 |
| *Eristalinus mendax* (Curran) | * | | | | | | 1 |
| *Eristalinus taeniops* (Wiedemann) | * | * | * | * | | * | 5 |
| *Phytomia incisa* (Wiedemann) | * | * | * | * | | * | 5 |
| *Phytomia natalensis* (Macquart) | * | | | | | | 1 |
| *Senaspis haemorrhoa* (Gerstaecker) | * | | | | | | 1 |
| *Simoides crassipes* (Fabricius) | * | | | | | | 1 |
| **Tachinidae** | | | | | | | |
| ?*Calozenillia perlucidia* (Karsch) | * | | | | | | 1 |
| ?*Pretoriamia* sp. 1 | * | | | | | | 1 |
| *Pales* sp. | * | | | | | | 1 |
| *Peleteria rustica* (Karsch) | | * | | | | | 1 |
| *Peleteria* sp. unknown | * | * | | | | | 2 |
| *Peribaea* sp. 1 | | * | | | | | 1 |

(d) Coleoptera (beetles)

| | brev | drep | etb | gerr | mell | nilo | No. species caught on |
|---|---|---|---|---|---|---|---|
| **Bruchidae** | | | | | | | |
| Bruchidae spp. | * | | | | * | * | 3 |
| **Buprestidae** | | | | | | | |
| Buprestidae spp. | * | | * | | | | 2 |
| **Cerambycidae** | | | | | | | |
| Cerambycinae sp. 1 | * | | | | | | 1 |
| Cerambycinae sp. 2 | * | | | | | | 1 |
| **Chrysomelidae** | | | | | | | |
| Gynandropthalma sp. | * | * | * | | | | 3 |
| Cryptocephalinae sp. 1 | | * | | | | | 1 |
| Cryptocephalinae sp. 2 | | * | | | | | 1 |
| Cryptocephalinae sp. 3 | * | | | | | | 1 |

| | brev | drep | etb | gerr | mell | nilo | No. species caught on |
|---|---|---|---|---|---|---|---|
| Cryptocephalinae sp. 4 | * | | | | | * | 2 |
| Clytrinae sp. 1 | | | | * | * | | 2 |
| Clytrinae sp. 3 | | | | | | * | 1 |
| ?*Monolepta ephipiata* | | * | | * | | | 2 |
| ?Alticinae sp. | | | * | | | | 1 |
| ?*Megalognatha meruensis* | | | | * | | | 1 |
| Galerucinae sp. 1 | | | | | | * | 1 |
| Galerucinae sp. 2 | | | | * | | | 1 |
| Galerucinae sp. 4 | | | | * | | | 1 |
| Galerucinae sp. 7 | | | | | | * | 1 |
| Galerucinae sp. 8 | | | | | | * | 1 |
| ?Galerucinae sp. | * | | | | | | 1 |
| Chrysomelidae sp. 1 | | | * | | | | 1 |
| **Coccinellidae** | | | | | | | |
| *Psyllobora nassata* (Erichson) | | * | | | | | 1 |
| **Curculionidae** | | | | | | | |
| *Curculionidae* sp. | * | | | | | | 1 |
| **Lycidae** | | | | | | | |
| *Lycus* sp. 1 | * | | | * | | * | 3 |
| *Lycus* sp. 2 | | | | | * | | 1 |
| *Lycus serenus* Kln. | * | | | * | | * | 3 |
| Lycidae | * | | | | | | 1 |
| **Meloidae** | | | | | | | |
| *Coryna* ?*apicornis* Guer. | * | | | | * | | 2 |
| *Coryna* ?*chevrolati* Beauc. | | | | | * | | 1 |
| **Prionoceridae** | | | | | | | |
| *Idgia* sp. | | | | * | | | 1 |
| **Scarabaeidae** | | | | | | | |
| ?*Diplognatha* sp. | | | | | * | | 1 |
| *Dichista cincta* de Geer | * | | | | * | | 2 |
| *Leucocelis* sp. | * | | | | * | | 2 |
| *Mausoleopsis amabilis* Gerstaecker | * | | | | * | | 2 |
| *Paleopragma* ?*petersil* Harold | * | | | | | | 1 |
| *Pachnoda elegantissima* Csiki | | | | * | | | 1 |
| *Rhabdotis sobrina* Gory & Percheron | * | | | * | * | | 3 |
| **Tenebrionidae** | | | | | | | |
| ?*Lagria* sp. | * | | | | | * | 2 |
| Alloculinae sp. | * | | | | | | 1 |
| Lagriinae sp. | * | | | | | | 1 |

(e) Lepidoptera (butterflies and moths)

| | brev | drep | etb | gerr | mell | nilo | No. species caught on |
|---|---|---|---|---|---|---|---|
| **Hesperiidae** | | | | | | | |
| Hesperiidae sp. | | | | | * | | 1 |
| **Lycaenidae** | | | | | | | |
| *Anthene amarah amarah* Guerin-Meneville | * | | * | * | | * | 4 |
| *Azanus jesous* Guerin-Meneville | * | * | | * | * | * | 5 |
| *Azanus natalensis* Trimen | | | | | * | | 1 |
| *Azanus ubaldus* Cramer | | * | * | | * | | 3 |
| *Leptotes pirithous* Linne | | | | | * | | 1 |
| *Axiocerses harpax uganda* Clench | | | | | | * | 1 |
| Lycaenidae spp. | * | | | * | * | * | 4 |
| **Nymphalidae** | | | | | | | |
| *Acraea* sp. 1 | * | | | | | | 1 |
| *Neocoenyra gregorii* Butler | * | | | | | | 1 |
| *Junonia hierta cebrene* Trimen | | | | | * | * | 2 |
| Nymphalidae sp. | | | | * | | | 1 |
| **Pieridae** | | | | | | | |
| *Belenois aurota aurota* Fabricius | * | | * | | | * | 3 |
| *Colotis aurigineus* Butler | | | * | | | * | 2 |
| Pieridae spp. | * | * | | | | | 2 |
| **Arctiidae** | | | | | | | |
| *Amata* nr. *chrysozona* | * | | | * | | | 2 |
| **Sphingidae** | | | | | | | |
| *Cephanodes hylas* (L.) | * | | | | | | 1 |
| | | | | | | | |
| unidentified moths | * | | | * | | * | 3 |

Appendix 7. Floral abundances recorded during surveys in each week of web sampling in 2004 at both sites.

(a) Turkana Boma

| **Family** | **Species** | **May** | | | **June** | | | **July** | | | **August** |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Week 1 | Week 2 | **Total** | Week 1 | Week 2 | **Total** | Week 1 | Week 2 | **Total** | Week 1 |
| Acanthaceae | *Barleria spinisepala* | | | **0** | 27 | 16 | **43** | 94 | 117 | **211** | **66** |
| Acanthaceae | *Justicia diclipteroides* | 45 | 73 | **118** | 6 | 8 | **14** | | | **0** | **11** |
| Acanthaceae | *Justicia lorata* | 161 | 146 | **307** | 5 | 12 | **17** | | | **0** | **46** |
| Acanthaceae | *Monechma* sp. B | 7 | 67 | **74** | 740 | 921 | **1661** | 2 | 2 | **4** | **35** |
| Acanthaceae | *Ruellia* sp. | 15 | 12 | **27** | 2 | | **2** | | | **0** | **105** |
| Amaranthaceae | *Aerva lanata* | | 180 | **180** | 298 | 194 | **492** | | | **0** | **76** |
| Apocynaceae | *Carissa edulis* | | | **0** | | | **0** | | | **0** | **4** |
| Asclepiadaceae | *Sarcostemma viminale* | | | **0** | | | **0** | | 180 | **180** | **0** |
| Asteraceae | Asteraceae spp. yellow | 76 | 104 | **180** | | | **0** | | | **0** | **0** |
| Asteraceae | *Emilia discifolia* | | | **0** | 10 | 1 | **11** | | | **0** | **2** |
| Asteraceae | *Felicia muricola* | 19 | 13 | **32** | | | **0** | | | **0** | **2** |
| Asteraceae | *Gutenbergia cordifolia* | 142 | 498 | **640** | 1321 | 440 | **1761** | 3 | | **3** | **11** |
| Asteraceae | *Helichrysum glumaceum* | 175 | 323 | **498** | 177 | 212 | **389** | | | **0** | **40** |
| Asteraceae | *Osteospermum vaillantii* | | | **0** | 5 | 4 | **9** | 4 | 7 | **11** | **53** |
| Balanitaceae | *Balanites* sp. | 260 | 600 | **860** | | | **0** | | | **0** | **0** |
| Caryophyllaceae | *Silene* sp. | 0 | 4 | **4** | | | **0** | | | **0** | **0** |
| Commelinaceae | *Commelina africana* | 26 | 15 | **41** | | | **0** | | | **0** | **0** |
| Commelinaceae | *Commelina reptans* | 131 | 20 | **151** | | | **0** | | | **0** | **4** |
| Commelinaceae | *Commelina* spp. blue | 1893 | 1237 | **3130** | 26 | 4 | **30** | 6 | 6 | **12** | **265** |
| Convolvulaceae | *Evolvulus alsinoides* | 170 | 128 | **298** | 41 | | **41** | | | **0** | **61** |
| Convolvulaceae | *Ipomoea ficifolia* | | | **0** | 6 | 7 | **13** | | | **0** | **0** |
| Convolvulaceae | *Ipomoea obscura* | 9 | 0 | **9** | 11 | 12 | **23** | | | **0** | **1** |
| Convolvulaceae | *Ipomoea ochracea* | 1 | 1 | **2** | 2 | | **2** | | | **0** | **0** |
| Convolvulaceae | *Ipomoea sinensis* | 33 | 20 | **53** | 9 | 10 | **19** | 1 | 1 | **2** | **17** |
| Convolvulaceae | *Ipomoea* sp. 1 | | 4 | **4** | | | **0** | | | **0** | **1** |
| Crassulaceae | *Kalanchoe* sp. 1 | | 13 | **13** | 284 | 479 | **763** | | | **0** | **0** |
| Euphorbiaceae | *Croton dichogamous* | 1538 | 540 | **2078** | | | **0** | | | **0** | **0** |

| **Family** | **Species** | **May** | | | **June** | | | **July** | | | **August** |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Week 1 | Week 2 | **Total** | Week 1 | Week 2 | **Total** | Week 1 | Week 2 | **Total** | Week 1 |
| Euphorbiaceae | *Euphorbia* sp. | | 12 | **12** | 140 | 299 | **439** | | | **0** | **1619** |
| Euphorbiaceae | *Phyllanthus sepialis* | | | **0** | | | **0** | | | **0** | **16540** |
| Fabaceae | *Senegalia brevispica* | 744 | 1310 | **2054** | 94 | 241 | **335** | 599 | 740 | **1339** | **5374** |
| Fabaceae | *Vachellia etbaica* | | | **0** | | | **0** | | | **0** | **5838** |
| Fabaceae | *Vachellia gerrardii* | 27 | 19 | **46** | | | **0** | | | **0** | **11** |
| Fabaceae | *Senegalia mellifera* | | | **0** | | | **0** | | | **0** | **0** |
| Fabaceae | *Vachellia nilotica* | | | **0** | | 5 | **5** | 3 | 7 | **10** | **0** |
| Fabaceae | *Indigofera volkensii* | 959 | 2145 | **3104** | 18 | 6 | **24** | | | **0** | **50** |
| Fabaceae | *Rhyncosia ?ferringunea* | | 5 | **5** | | | **0** | | | **0** | **0** |
| Fabaceae | *Vigna* sp. | 2 | 1 | **3** | | | **0** | | | **0** | **0** |
| Lamiaceae | ?*Becium* sp. | 91 | 65 | **156** | 7 | | **7** | | | **0** | **25** |
| Lamiaceae | *Leucas glabrata* | 1128 | 293 | **1421** | 129 | 79 | **208** | | | **0** | **704** |
| Lamiaceae | *Leucas* sp. 2 | | | **0** | 43 | | **43** | | | **0** | **0** |
| Lamiaceae | *Ocimum forskolei* | 3677 | 3370 | **7047** | 571 | 14 | **585** | | | **0** | **363** |
| Lamiaceae | *Ocimum* sp. 2 | | | **0** | | 18 | **18** | | | **0** | **0** |
| Lamiaceae | *Plectranthus caninus* | 10 | 48 | **58** | 276 | 115 | **391** | | | **0** | **0** |
| Lamiaceae | *Plectranthus longipes* | 175 | 120 | **295** | | | **0** | | | **0** | **0** |
| Liliceae | *Chlorophytum* sp. | 0 | 10 | **10** | 1 | | **1** | | | **0** | **0** |
| Malvaceae | *Abutilon mauritianum* | 368 | 402 | **770** | 89 | 74 | **163** | 2 | 4 | **6** | **352** |
| Malvaceae | *Hibiscus aponeurus* | 6 | 5 | **11** | 7 | 3 | **10** | | | **0** | **19** |
| Malvaceae | *Hibiscus flavifolius* | 69 | 56 | **125** | 94 | 7 | **101** | | | **0** | **105** |
| Malvaceae | *Hibiscus vitifolius* | 6 | 8 | **14** | 6 | 2 | **8** | | | **0** | **1** |
| Malvaceae | *Pavonia gallaensis* | 169 | 310 | **479** | 61 | 11 | **72** | 1 | 5 | **6** | **201** |
| Malvaceae | *Sida ovata* | 13 | 52 | **65** | 4 | 4 | **8** | | | **0** | **51** |
| Malvaceae | *Sida schimperiana* | | | **0** | | | **0** | | | **0** | **16** |
| Polygalaceae | *Polygala sphenoptera* | 409 | 322 | **731** | 18 | 2 | **20** | 1 | 2 | **3** | **247** |
| Portulacaceae | *Portulaca* spp. | | 12 | **12** | | | **0** | | | **0** | **2** |
| Portulacaceae | *Talinum portulacifolium* | 2 | 1 | **3** | | | **0** | | | **0** | **0** |
| Rubiaceae | *Pentanisia ouranogyne* | 2575 | 6035 | **8610** | 28 | | **28** | 8 | | **8** | **131** |
| Scrophulariaceae | *Craterostigma* sp. 1 | 343 | 5 | **348** | | | **0** | | | **0** | **72** |
| Scrophulariaceae | *Craterostigma* sp. 2 | | | **0** | | | **0** | | | **0** | **21** |

| **Family** | **Species** | **May** | | | **June** | | | **July** | | | **August** |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Week 1 | Week 2 | **Total** | Week 1 | Week 2 | **Total** | Week 1 | Week 2 | **Total** | Week 1 |
| Solanaceae | *Solanum* sp. 1 | 43 | 85 | **128** | 22 | 10 | **32** | | | **0** | **33** |
| Sterculiaceae | *Melhania ovata* | 16 | 148 | **164** | 10 | | **10** | | | **0** | **6** |
| Sterculiaceae | *Melhania velutina* | | 1 | **1** | 2 | | **2** | | | **0** | **2** |
| Tiliaceae | *Grewia* spp. | 9 | 1 | **10** | 13 | | **13** | | 21 | **21** | **49** |
| Verbenaceae | *Lippia kituiensis* | 2029 | 46687 | **48716** | 1658 | 1 | **1659** | | | **0** | **1484** |
| Verbenaceae | *Priva curtisiae* | 35 | 50 | **85** | | | **0** | | | **0** | **0** |
| Vitaceae | *Cyphostemma serpens* | | 41 | **41** | 9 | 7 | **16** | | | **0** | **0** |
| Zygophyllaceae | *Tribulus terrestris* | 2 | 0 | **2** | | | **0** | | | **0** | **0** |
| | unknown sp. 1 | 10 | 0 | **10** | | | **0** | | | **0** | **0** |
| | unknown sp. 2 | 22 | 4 | **26** | | | **0** | | | **0** | **0** |
| | unknown sp. 3 | | | **0** | | | **0** | | | **0** | **3** |
| | unknown sp. 4 | | | **0** | | | **0** | | | **0** | **1** |
| | unknown sp. 5 | | | **0** | | | **0** | | | **0** | **79** |
| | unknown sp. 6 | | | **0** | | | **0** | | | **0** | **25** |
| **Total floral units** | | 17640 | 65621 | **83261** | 6270 | 3218 | **9475** | 724 | 1090 | **1814** | **34224** |

(b) Junction

| **Family** | **Species** | **June** | | | **July** | | |
|---|---|---|---|---|---|---|---|
| | | Week 1 | Week 2 | **Total** | Week 1 | Week 2 | **Total** |
| Acanthaceae | *Barleria spinisepala* | 36 | 99 | **135** | 711 | 207 | **918** |
| Acanthaceae | *Hypoestes forskahlii* | 570 | 351 | **921** | 109 | 41 | **150** |
| Acanthaceae | *Justicia lorata* | 1123 | 263 | **1386** | | | **0** |
| Acanthaceae | *Monechma* sp. B | 1096 | 2964 | **4060** | 7 | 7 | **14** |
| Anacardiaceae | *Rhus natalensis* | 7 | | **7** | | | **0** |
| Apocynaceae | *Carissa edulis* | | | **0** | 23 | | **23** |
| Asteraceae | Compositae sp. 1 | 3 | 1 | **4** | | | **0** |
| Asteraceae | *Emilia discifolia* | 1191 | 665 | **1856** | 5 | 1 | **6** |
| Asteraceae | *Gutenbergia cordifolia* | 171 | 165 | **336** | | | **0** |
| Asteraceae | *Helichrysum glumaceum* | 2822 | 2317 | **5139** | | | **0** |
| Asteraceae | *Helichrysum* sp. 2 | | 3 | **3** | | | **0** |
| Asteraceae | *Osteospermum vaillantii* | 64 | 63 | **127** | 5 | 1 | **6** |
| Asteraceae | *Tagetes minuta* | | 36 | **36** | | | **0** |
| Boraginaceae | *Echiochilon lithospermoides* | 501 | 433 | **934** | 15 | 16 | **31** |
| Boraginaceae | *Heliotropium steudneri* | 2725 | 1126 | **3851** | | | **0** |
| Boraginaceae | *Heliotropium strigosum* | 1785 | 781 | **2566** | 6 | | **6** |
| Boraginaceae | *Heliotropium zeylanicum* | 113 | 143 | **256** | | | **0** |
| Caryophyllaceae | *Silene* sp. | 1 | 8 | **9** | | | **0** |
| Convolvulaceae | *Evolvulus alsinoides* | 54 | 12 | **66** | 7 | | **7** |
| Convolvulaceae | *Ipomoea hildebrantii* | 45 | 18 | **63** | | | **0** |
| Convolvulaceae | *Ipomoea kituiensis* | 3 | 24 | **27** | | | **0** |
| Convolvulaceae | *Ipomoea ochracea* | 1 | 2 | **3** | | | **0** |
| Convolvulaceae | *Ipomoea sinensis* | 86 | 93 | **179** | 10 | 4 | **14** |
| Crassulaceae | *Kalanchoe* sp. 2 | | | **0** | 9 | 2 | **11** |
| Euphorbiaceae | *Croton dichogamous* | 18 | | **18** | | | **0** |
| Ebenaceae | *Euclea* sp. | | 483 | **483** | | | **0** |
| Fabaceae | *Senegalia brevispica* | 34 | 29 | **63** | 57 | 23 | **80** |
| Fabaceae | *Vachellia drepanolobium* | 2 | | **2** | | | **0** |

| **Family** | **Species** | **June** | | | **July** | | |
|---|---|---|---|---|---|---|---|
| | | Week 1 | Week 2 | **Total** | Week 1 | Week 2 | **Total** |
| Fabaceae | *Vachellia etbaica* | | | **0** | | | **0** |
| Fabaceae | *Cassia mimosoides* | 93 | 69 | **162** | | | **0** |
| Fabaceae | *Indigofera volkensii* | 77 | 36 | **113** | | | **0** |
| Fabaceae | Legume sp. 1 | 7 | 13 | **20** | | | **0** |
| Lamiaceae | ?*Becium* sp. | 13 | 3 | **16** | | | **0** |
| Lamiaceae | *Endostemon tereticaulis* | 458 | 63 | **521** | | | **0** |
| Lamiaceae | *Leucas glabrata* | 660 | 924 | **1584** | | | **0** |
| Lamiaceae | *Ocimum forskolei* | 106 | 5 | **111** | | | **0** |
| Lamiaceae | *Plectranthus caninus* | 13 | 11 | **24** | | | **0** |
| Malvaceae | *Pavonia gallaensis* | 217 | 95 | **312** | 10 | 3 | **13** |
| Malvaceae | *Sida ovata* | 56 | 14 | **70** | | | **0** |
| Malvaceae | *Sida schimperiana* | 2 | 2 | **4** | | | **0** |
| Meliaceae | *Turraea mombassana* | 11 | 5 | **16** | | | **0** |
| Polygalaceae | *Polygala* sp. 2 | 132 | 143 | **275** | | | **0** |
| Polygalaceae | *Polygala sphenoptera* | 26 | 11 | **37** | | | **0** |
| Rubiaceae | *Pentanisia ouranogyne* | 24 | | **24** | | | **0** |
| Solanaceae | *Solanum* sp. 1 | 13 | 6 | **19** | | | **0** |
| Sterculiaceae | *Melhania ovata* | 65 | 15 | **80** | | | **0** |
| Tiliceae | *Grewia* spp. | 13 | 3 | **16** | | | **0** |
| Verbenaceae | *Lippia kituiensis* | 1462 | 587 | **2049** | | | **0** |
| Verbenaceae | *Priva curtisiae* | 4 | | **4** | | | **0** |
| | unknown sp. 7 | 2 | | **2** | | | **0** |
| | unknown sp. 8 | 1 | | **1** | | | **0** |
| | unknown sp. 9 | 41 | | **41** | | | **0** |
| | unknown sp. 10 | | 11 | **11** | | | **0** |
| | unknown sp. 11 | | 40 | **40** | | | **0** |
| | unknown sp. 12 | | | **0** | 2 | | **2** |
| **Total floral units** | | 15947 | 12135 | **28082** | 976 | 305 | **1281** |

Appendix 8. Visitor types, level of identification and the flower-visitor interaction webs in which each was recorded. 1: May, 2: June. 3: July, 4: August. Identification levels: s: species, m: morphospecies, g: morphogroup, u: unknown group.

| **Family** | **Visitor species** | | **Turkana Boma** | | | | **Junction** | |
|---|---|---|---|---|---|---|---|---|
| | | | **1** | **2** | **3** | **4** | **2** | **3** |
| **Hymenoptera** | | | | | | | | |
| **bees** | | | | | | | | |
| Andrenidae | *Melitturga minima* | s | 1 | | | | | |
| Apidae | *Amegilla calens* | s | | 2 | | | 2 | |
| Apidae | *Amegilla capensis* | s | | | | | 2 | |
| Apidae | *Amegilla penicula* | s | | | | 4 | 2 | 3 |
| Apidae | *Anthophora pygmaea* | s | | | | | 2 | |
| Apidae | *Apis mellifera* | s | 1 | 2 | 3 | 4 | 2 | |
| Apidae | *Ceratina minuta* | s | 1 | | | | | |
| Apidae | *Ceratina moerenhouti* | s | 1 | 2 | | | 2 | |
| Apidae | *Ceratina nyassensis* | s | | 2 | 3 | 4 | | 3 |
| Apidae | unknown *Ceratina* sp. | g | 1 | | | | | |
| Apidae | *Hypotrigona ruspolii* | s | | 2 | | | | |
| Apidae | large Apidae spp. | g | 1 | 2 | | 4 | 2 | 3 |
| Apidae | *Macrogalea candida* | s | 1 | 2 | | | | |
| Apidae | *Plebeina hildebrantii* | s | 1 | 2 | | 4 | | |
| Apidae | *Tetralonia boharti* | s | 1 | | | | | |
| Apidae | *Tetralonia nigropilosa* | s | | | | | 2 | |
| Apidae | *Tetraloniella abrochia* | s | 1 | | | | | |
| Apidae | *Thyreus calceatus* | s | | | | | 2 | |
| Apidae | *Xylocopa somalica* | s | | | | 4 | 2 | |
| Colletidae | *Colletes* sp. 2 | s | | | | | 2 | |
| Colletidae | *Hylaeus* sp. b | s | | 2 | | | | |
| Colletidae | ?*Hylaeus* sp. | g | | 2 | 3 | | | |
| Halictidae | *Halictus* (*Seladonia*) sp. 1 | s | 1 | 2 | | | 2 | 3 |
| Halictidae | *Halictus* (*Seladonia*) sp. 2 | s | | 2 | | | | |
| Halictidae | *Halictus* (*Seladonia*) sp. C | s | | 2 | | | | |
| Halictidae | *Lasioglossum* (*Dialictus*) sp. 1 | s | 1 | | | | | 3 |
| Halictidae | *Lasioglossum* (*Dialictus*) sp. 2 | s | | 2 | | | | |
| Halictidae | *Lasioglossum* sp. B | s | | 2 | | | | |
| Halictidae | *Lipotriches* (*Lipotriches*) sp. 1 | s | 1 | 2 | | 4 | | |
| Halictidae | ?*Lipotriches* sp. 1 | m | | | | | 2 | |
| Halictidae | *Lipotriches* (*Lipotriches*) sp. A | s | | 2 | | | | |
| Halictidae | *Lipotriches* (*Lipotriches*) sp. B | s | 1 | | | | | |
| Halictidae | *Lipotriches* (*Lipotriches*) sp. C | s | | | | | 2 | |
| Halictidae | *Lipotriches* (*Lipotriches*) sp. D | s | 1 | | | | | |
| Halictidae | *Lipotriches* (*Lipotriches*) sp. G | s | | | | | 2 | |
| Halictidae | *Lipotriches* (*Lipotriches*) sp. H | s | | 2 | | | 2 | |
| Halictidae | *Lipotriches* (*Lipotriches*) sp. L | s | 1 | | | | | |
| Halictidae | *Lipotriches* (*Lipotriches*) sp. M | s | | | | | 2 | |
| Halictidae | *Lipotriches* sp. A | s | | | | | 2 | |
| Halictidae | *Patellapis* (*Zonalictus*) sp. 1 | s | 1 | | | 4 | | |
| Halictidae | *Patellapis* sp. A | s | | 2 | | | 2 | |
| Halictidae | *Patellapis* sp. C | s | | 2 | | 4 | | |

| Family | Visitor species | | Turkana Boma | | | | Junction | |
|---|---|---|---|---|---|---|---|---|
| | | | **1** | **2** | **3** | **4** | **2** | **3** |
| Halictidae | *Pseudapis* (*Pseudapis*) sp. 1 | s | 1 | | 3 | 4 | 2 | 3 |
| Halictidae | *Pseudapis* (*Pseudapis*) sp. 2 | s | 1 | | | | | |
| Halictidae | *Systropha* sp. 1 | s | | | | | 2 | |
| Halictidae | Halictidae sp. 1 | m | 1 | | | | | |
| Halictidae | Halictidae sp. 2 | m | 1 | | | | | |
| Halictidae | Halictidae sp. 3 | m | | | | | 2 | |
| Halictidae | Halictidae sp. 4 | m | | | | | 2 | |
| Halictidae | unknown Halictidae spp. | g | | 2 | | 4 | | 3 |
| Megachilidae | ?*Aspidosmia* sp. 1 | s | | | | | 2 | |
| Megachilidae | ?*Ichteranthidium* sp. 1 | s | 1 | | | | 2 | |
| Megachilidae | Anthidiini sp. 1 | s | | | | | 2 | |
| Megachilidae | *Heriades* (*Heriades*) sp. 1 | s | 1 | 2 | | | 2 | |
| Megachilidae | *Heriades* sp. a | s | | 2 | | | 2 | |
| Megachilidae | Megachildae sp. large | m | 1 | | | | | |
| Megachilidae | *Megachile* (?*Pseudomegachile*) sp. 1 | s | | 2 | | | | |
| Megachilidae | *Megachile* (*Chalicodoma*) sp. 2 | s | 1 | 2 | | 4 | | |
| Megachilidae | *Megachile* (*Chalicodoma*) spp. small | g | 1 | 2 | | | 2 | |
| Megachilidae | Osmiini sp. a | s | | 2 | | | | |
| Megachilidae | Osmiini sp. d | s | | | 3 | | | |
| Megachilidae | Osmiini sp. e | s | 1 | | | | 2 | |
| Megachilidae | Osmiini sp. g | s | 1 | | | | | |
| Megachilidae | Osmiini sp. j | s | | | | | | 3 |
| Megachilidae | unknown Osmiini spp. | g | 1 | | | | 2 | |
| | med bee spp. | u | 1 | 2 | | | 2 | 3 |
| | small bee spp. | u | 1 | 2 | | | 2 | 3 |
| | small green bee spp. | u | | | | | | 3 |
| | unknown bee spp. | u | 1 | 2 | | | 2 | 3 |
| | unknown bee sp. 1 | u | 1 | | | | | |
| | unknown small black bee | u | | | 3 | | | |
| **wasps** | | | | | | | | |
| Chrysididae | Chrysididae spp. | g | | 2 | | 4 | 2 | |
| Eumenidae | Eumenidae sp. 3 | m | | 2 | | | | |
| Eumenidae | Eumenidae sp. 4 | m | | | 3 | | | |
| Eumenidae | Eumenidae sp. 8 | m | | 2 | | | 2 | |
| Eumenidae | Eumenidae sp. 9 | m | | | | | 2 | 3 |
| Eumenidae | Eumenidae sp. 13 | m | 1 | 2 | | | | |
| Eumenidae | Eumenidae sp. 14 | m | | 2 | | | | |
| Eumenidae | Eumenidae sp. 15 | m | | | | | 2 | |
| Eumenidae | Eumenidae sp. 16 | m | | | | | 2 | |
| Vespidae | *Polistes* sp. | m | 1 | | | | | |
| Vespidae | ?*Polistes* sp. | m | | | | | 2 | |
| Ichneumonidae | Ichneumonidae sp. | m | | | | 4 | | |
| Pompilidae | Pompilidae sp. 2 | m | | | | | 2 | |
| Scoliidae | *Cathimeris* sp. | m | | | | | | 3 |
| Sphecidae | *Ammophila* sp. 1 | m | | | | | 2 | |
| Sphecidae | *Cerceris* sp. 2 | m | | 2 | | 4 | | 3 |
| Sphecidae | *Cerceris* sp. 4 | m | 1 | | | | | |
| Sphecidae | *Liris* sp. 1 | m | | | | 4 | | |

| **Family** | **Visitor species** | | **Turkana Boma** | | | | **Junction** | |
|---|---|---|---|---|---|---|---|---|
| | | | **1** | **2** | **3** | **4** | **2** | **3** |
| Sphecidae | *Philanthus* sp. 3 | m | | | | | 2 | |
| Sphecidae | *Sphex* spp. | g | 1 | | | | | |
| Sphecidae | *Tachysphex* sp. 1 | m | | 2 | 3 | | | |
| Sphecidae | ?*Tachysphex* sp. 1 | m | | | 3 | | | |
| Sphecidae | *Tachytes* sp. 1 | m | | 2 | | | | |
| Sphecidae | unknown Sphecidae sp. | g | 1 | | | | | 3 |
| | unknown wasp spp. | u | 1 | 2 | | 4 | 2 | 3 |
| | wasp sp. 1 | m | | | | 4 | | |
| | wasp sp. 2 | m | | 2 | | | | |
| **ants** | | | | | | | | |
| Formicidae | Formicidae spp. | g | 1 | 2 | 3 | 4 | 2 | |
| **Diptera** | | | | | | | | |
| Bombyliidae | *Bombomyia discoidea* | s | | | | 4 | | |
| Bombyliidae | Bombyliidae spp. | g | 1 | | | 4 | 2 | |
| Bombyliidae | Bombyliidae sp. 1 | m | 1 | | | | | |
| Bombyliidae | Bombyliidae sp. 2 | m | 1 | | | | | |
| Bombyliidae | *Bombylisoma nucale* | s | 1 | | | | | |
| Bombyliidae | Gonarthrus sp. 1 | s | | 2 | | | | |
| Bombyliidae | *Villa paniscoides* | s | | | | | | |
| Calliphoridae | *Hemipyrellia fernandica* | s | | | | | | |
| Calliphoridae | *Isomyia tristis* | s | 1 | | | | | |
| Calliphoridae | *Rhyncomya* spp. | g | | | 3 | 4 | | 3 |
| Calliphoridae | unknown Calliphoridae spp. | g | 1 | | | | | |
| Chloropidae | Chloropidae sp. 1 | s | | 2 | | | | |
| Culicidae | Culicidae spp. | g | | 2 | | | | |
| Muscidae | *Coenosia cuthbertsoni* | s | | | | | 2 | |
| Muscidae | *Coenosia exigua* | s | | 2 | | | | |
| Muscidae | *Limnophora quaterna* | s | | 2 | | | | |
| Muscidae | *Musca domestica curviforceps* | s | 1 | | | | | |
| Mysotophilidae | Mysotophilidae sp. | m | 1 | | | | | |
| Sarcophagidae | *Hoplacephala inermis* | s | | | | | | 3 |
| Sarcophagidae | Miltogramminae spp. | g | | | | 4 | | |
| Sarcophagidae | Sarcophagidae sp. | g | 1 | | | | | |
| Syrphidae | *Eristalinus mendax* | s | 1 | | | | | |
| Syrphidae | *Eristalinus taeniops* | s | 1 | | | | | |
| Syrphidae | *Eumerus* nr. *armipes* | s | | | | | | |
| Syrphidae | *Eumerus obliquus* | s | | 2 | | | | |
| Syrphidae | *Phytomia incisa* | s | 1 | | | | | |
| Syrphidae | unknown *Eristalinus* sp. | g | 1 | | | | | |
| Syrphidae | unknown Syrphidae spp. | g | 1 | | | | 2 | |
| Tachinidae | ?*Compsilura concinnata* | s | | | | | | |
| Tachinidae | ?*Exorista* sp. | s | 1 | | | | | |
| Tachinidae | *Pretoriamyia* sp. 1 | m | 1 | | | | | |
| Tachinidae | unknown Tachinidae spp. | g | 1 | | | | | |
| Tephritidae | Tephritidae spp. | g | | | 3 | | 2 | |
| | tiny Diptera spp. | u | | 2 | | | | |
| | unknown Diptera spp. | u | 1 | | 3 | 4 | 2 | |

| **Family** | **Visitor species** | | **Turkana Boma** | | | | **Junction** | |
|---|---|---|---|---|---|---|---|---|
| | | | **1** | **2** | **3** | **4** | **2** | **3** |
| **Coleoptera** | | | | | | | | |
| Bruchidae | Bruchidae spp. | g | | 2 | | | | |
| Buprestidae | Buprestidae sp. 1 | m | | | 3 | | | |
| Cerambycidae | Cerambycidae sp. 1 | m | 1 | 2 | | | | |
| Cerambycidae | Cerambycidae sp. 2 | m | 1 | | | | | |
| Cerambycidae | Lamiinae sp.1 | m | | | | | 2 | |
| Chrysomelidae | ?Alticinae sp. 1 | m | 1 | | | | | |
| Chrysomelidae | Alticinae sp. 1 | m | 1 | 2 | | | 2 | |
| Chrysomelidae | Alticinae sp. 2 | m | | 2 | | | | |
| Chrysomelidae | Chrysomelidae sp. 1 | m | 1 | | | | | |
| Chrysomelidae | Clytrinae sp. 1 | m | 1 | | | | | |
| Chrysomelidae | Clytrinae sp. 3 | m | | 2 | | | | |
| Chrysomelidae | Clytrinae sp. 4 | m | | | | | 2 | |
| Chrysomelidae | Clytrinae sp. 5 | m | | 2 | | | | |
| Chrysomelidae | Galerucinae sp. 11 | m | 1 | | | | | |
| Chrysomelidae | Galerucinae sp. 5 | m | | 2 | | | | |
| Chrysomelidae | Galerucinae sp. 6 | m | 1 | | | | | |
| Chrysomelidae | *Megalognatha meruensis* | s | 1 | 2 | | | 2 | |
| Curculionidae | Curculionidae sp. | s | 1 | | | | | |
| Lycidae | *Lycus serenus* | s | 1 | 2 | | | | |
| Lycidae | *Lycus* sp. 1 | s | 1 | | | | | |
| Meloidae | *Coryna ?ambigua* | m | 1 | | 3 | | | |
| Meloidae | *Coryna ?apicornis* | m | | 2 | | | | |
| Meloidae | *Coryna ?chevrolati* | m | 1 | | | | 2 | |
| Meloidae | unknown *Coryna* spp. | g | 1 | 2 | | | | |
| Phalacridae | Phalacridae sp. | m | | | | | 2 | |
| Prionoceridae | *Idgia* sp. | m | 1 | | | | 2 | |
| Scarabaeidae | *Rhabdotis sobrina* | s | 1 | | | | | |
| | unknown Coleoptera sp. | u | | | | | 2 | |
| **Lepidoptera** | | | | | | | | |
| Arctiidae | Arctiidae sp. | m | 1 | | | | | |
| Hesperiidae | *Saragnesa phidyle* | s | 1 | 2 | | | | |
| Hesperiidae | *Spialia mata higginsi* | s | | | | | | 3 |
| Hesperiidae | *Spiralia* sp. | s | 1 | | | | | |
| Lycaenidae | *Anthene amarah amarah* | s | | 2 | | | | |
| Lycaenidae | *Azanus jesous* | s | | | | | 2 | |
| Lycaenidae | *Eicochrysops masai* | s | | 2 | | | | |
| Lycaenidae | *Freyeria trochylus trochylus* | s | | 2 | | | 2 | |
| Lycaenidae | Lycaenidae spp. | g | 1 | 2 | | | 2 | |
| Pieridae | *Belenois aurota aurota* | s | | | | | | 3 |
| Pieridae | *Eurema brigitta brigitta* | s | | | | | 2 | 3 |
| Pieridae | Pieridae spp. | g | 1 | 2 | | 4 | 2 | |
| Sphingidae | *Cephanodes hylas* | s | 1 | | | | | |
| | unknown butterfly spp. | g | 1 | 2 | | | | |
| | unknown moth sp. | g | 1 | | | | | |
| **Hemiptera** | | | | | | | | |
| | Hemiptera spp. juvenile | u | | | 3 | | | |
| | unknown Hemiptera spp. | u | 1 | | | 4 | | |

Appendix 9. Flower-visitor interactions in each seasonal web and the time periods in which they occurred.

(a) Turkana Boma, May

| Plant species | Visitor species | | TP1 | TP2 | TP3 | TP4 |
|---|---|---|---|---|---|---|
| *Senegalia brevispica* | bee | *Apis mellifera* | | | x | |
| *Croton dichogamous* | bee | *Apis mellifera* | | | | x |
| *Lippia kituiensis* | bee | *Apis mellifera* | | | | x |
| *Ocimum forskolei* | bee | *Apis mellifera* | | | x | x |
| *Justicia diclipteroides* | bee | *Plebeina hildebranti* | | x | | |
| *Abutilon mauritianum* | bee | *Tetralonia boharti* | | x | | |
| *Hibiscus flavifolius* | bee | *Tetralonia boharti* | | x | | |
| *Plectranthus longipes* | bee | *Tetraloniella abrochia* | | x | | |
| *Abutilon mauritianum* | bee | large Apidae spp. | | x | | |
| *Commelina spp. blue* | bee | large Apidae spp. | x | | | |
| *Indigofera volkensii* | bee | large Apidae spp. | x | | | |
| *Leucas glabrata* | bee | large Apidae spp. | | x | | |
| *Plectranthus longipes* | bee | large Apidae spp. | | x | | |
| *Rhyncosia ?ferrunginea* | bee | large Apidae spp. | | x | | |
| *Justicia diclipteroides* | bee | *Ceratina minuta* | | | x | |
| *Sida ovata* | bee | *Ceratina moerenhouti* | | x | | |
| *Ocimum forskolei* | bee | unknown *Ceratina* sp. | | | | x |
| *Gutenbergia cordifolia* | bee | *Macrogalea candida* | | | x | |
| *Plectranthus longipes* | bee | *Lipotriches (Lipotriches)* sp. 1 | | | | x |
| *Indigofera volkensii* | bee | *Lipotriches (Lipotriches)* sp. B | | x | x | |
| *Indigofera volkensii* | bee | *Lipotriches (Lipotriches)* sp. B | | | x | |
| *Gutenbergia cordifolia* | bee | *Lipotriches (Lipotriches)* sp. D | | | x | |
| *Indigofera volkensii* | bee | *Lipotriches (Lipotriches)* sp. L | | x | | |
| *Senegalia brevispica* | bee | *Pseudapis (Pseudapis)* sp. 1 | | | x | |
| *Indigofera volkensii* | bee | *Pseudapis (Pseudapis)* sp. 1 | | x | | |
| *Melhania ovata* | bee | *Pseudapis (Pseudapis)* sp. 1 | | | x | |
| *Croton dichogamous* | bee | *Pseudapis (Pseudapis)* sp. 2 | | | x | |
| *Hibiscus vitifolius* | bee | *Lasioglossum (Dialictus)* sp. 1 | | x | | |
| *Ipomoea sinensis* | bee | *Lasioglossum (Dialictus)* sp. 1 | x | x | | |
| *?Becium sp.* | bee | *Halictus (Seladonia)* sp. 1 | | x | | |
| *Evolvulus alsinoides* | bee | *Halictus (Seladonia)* sp. 1 | | x | | |
| *Justicia lorata* | bee | *Halictus (Seladonia)* sp. 1 | | | x | |
| *Felicia muricola* | bee | *Patellapis (Zonalictus)* sp. 1 | | x | | |
| *Ocimum forskolei* | bee | *Patellapis (Zonalictus)* sp. 1 | | x | | |
| *Ocimum forskolei* | bee | Halictidae sp. 1 | | | x | |
| *Leucas glabrata* | bee | Halictidae sp. 2 | x | | | |
| *Rhyncosia ?ferrunginea* | bee | Megachildae sp. large | | | x | |
| *Gutenbergia cordifolia* | bee | *Megachile (Chalicodoma)* sp. 2 | | | x | |
| *Ocimum forskolei* | bee | *Megachile (Chalicodoma)* sp. 2 | | | x | |
| *Rhyncosia ?ferrunginea* | bee | *Megachilidae (Chalicodoma)* sp. small | | | x | |
| *Ocimum forskolei* | bee | *Heriades (Heriades)* sp. 1 | | | x | |
| Asteraceae spp. yellow | bee | Osmiini sp. e | | x | | |
| *Gutenbergia cordifolia* | bee | Osmiini sp. e | | x | x | |
| *Gutenbergia cordifolia* | bee | Osmiini sp. g | | | x | |
| *Gutenbergia cordifolia* | bee | unknown Osmiini sp. | | | x | |

| Plant species | Visitor species | | TP1 | TP2 | TP3 | TP4 |
|---|---|---|---|---|---|---|
| *Indigofera volkensii* | bee | ? *Ichteranthidium* sp. 1 | | | x | |
| *Justicia lorata* | bee | *Melitturga minima* | | x | | |
| *Justicia lorata* | bee | med bee spp. | | x | x | |
| *Solanum* sp. 1 | bee | med bee spp. | | | x | |
| *Abutilon mauritianum* | bee | small bee spp. | | | x | |
| *Croton dichogamous* | bee | small bee spp. | | x | | |
| *Justicia diclipteroides* | bee | small bee spp. | | x | | |
| *Melhania velutina* | bee | small bee spp. | | | x | |
| *Monechma* sp. B | bee | small bee spp. | | | x | |
| *Craterostigma* sp. 1 | bee | unknown bee sp. 1 | | x | | |
| *Justicia lorata* | bee | unknown bee sp. 1 | | x | | |
| *Abutilon mauritianum* | bee | unknown bee spp. | | x | | |
| *Senegalia brevispica* | bee | unknown bee spp. | | | x | |
| Asteraceae spp. yellow | bee | unknown bee spp. | | x | | |
| *Gutenbergia cordifolia* | bee | unknown bee spp. | | x | x | |
| *Helichrysum glumaceum* | bee | unknown bee spp. | | x | | |
| *Ipomoea sinensis* | bee | unknown bee spp. | | x | | |
| *Justicia lorata* | bee | unknown bee spp. | | x | | |
| *Ocimum forskolei* | bee | unknown bee spp. | | x | x | |
| *Plectranthus longipes* | bee | unknown bee spp. | | | | x |
| *Polygala sphenoptera* | bee | unknown bee spp. | | x | | |
| *Priva curtisiae* | bee | unknown bee spp. | | x | | |
| Asteraceae spp. yellow | wasp | Eumenidae sp. 13 | | x | | |
| *Felicia muricola* | wasp | *Cerceris* sp. 4 | | | x | |
| *Senegalia brevispica* | wasp | *Sphex* spp. | | | x | x |
| *Lippia kituiensis* | wasp | *Sphex* spp. | | x | | |
| *Senegalia brevispica* | wasp | unknown Sphecidae sp. | | | | x |
| *Lippia kituiensis* | wasp | *Polistes* sp. | | | | x |
| *Abutilon mauritianum* | wasp | unknown wasp sp. | | | x | |
| *Gutenbergia cordifolia* | wasp | unknown wasp sp. | | x | | |
| *Evolvulus alsinoides* | fly | Bombyliidae sp. 1 | | x | | |
| *Helichrysum glumaceum* | fly | Bombyliidae sp. 1 | | x | | |
| *Melhania ovata* | fly | Bombyliidae sp. 2 | | | x | |
| *Pentanisia ouranogyne* | fly | Bombyliidae sp. 2 | | x | | |
| *Felicia muricola* | fly | Bombyliidae spp. | | x | | |
| *Helichrysum glumaceum* | fly | Bombyliidae spp. | | x | | |
| *Pentanisia ouranogyne* | fly | Bombyliidae spp. | | | x | |
| *Pentanisia ouranogyne* | fly | *Bombylisoma nucale* | | | x | |
| *Commelina spp. blue* | fly | *Isomyia tristis* | | x | | |
| *Balanites* sp. | fly | unknown Calliphoridae sp. | x | | | |
| *Vachellia gerrardii* | fly | *Eristalinus mendax* | | x | | |
| *Senegalia brevispica* | fly | *Eristalinus taeniops* | | x | | |
| Asteraceae spp. yellow | fly | *Eristalinus taeniops* | | x | | |
| *Senegalia brevispica* | fly | unknown *Eristalinus* sp. | | x | | |
| *Senegalia brevispica* | fly | *Phytomia incisa* | | x | x | x |
| *Croton dichogamous* | fly | *Phytomia incisa* | | x | | |
| *Lippia kituiensis* | fly | *Phytomia incisa* | x | | x | |
| *Lippia kituiensis* | fly | unknown Syrphidae sp. | | x | | |
| *Vachellia gerrardii* | fly | *Musca domestica curviforceps* | | | x | |
| *Asteraceae spp. yellow* | fly | Mysotophilidae sp. | | x | | |

| **Plant species** | **Visitor species** | | **TP1** | **TP2** | **TP3** | **TP4** |
|---|---|---|---|---|---|---|
| *Balanites sp.* | fly | Mysotophilidae sp. | x | x | x | x |
| *Felicia muricola* | fly | Mysotophilidae sp. | | | | x |
| *Lippia kituiensis* | fly | Mysotophilidae sp. | | x | x | |
| *Solanum* sp. 1 | fly | Mysotophilidae sp. | | x | | |
| *Senegalia brevispica* | fly | *Pretoriamyia* sp. 1 | x | x | | |
| *Vachellia gerrardii* | fly | *Pretoriamyia* sp. 1 | x | x | x | |
| *Balanites* sp. | fly | ?*Exorista* sp. | | x | | |
| *Balanites* sp. | fly | unknown Tachinidae sp. | | | x | |
| *Balanites* sp. | fly | Sarcophagidae sp. | | | x | |
| *Senegalia brevispica* | fly | unknown Diptera spp. | x | x | | |
| *Vachellia gerrardii* | fly | unknown Diptera spp. | | | x | |
| Asteraceae spp. yellow | fly | unknown Diptera spp. | | x | | |
| *Ocimum forskolei* | fly | unknown Diptera spp. | | | x | |
| *Abutilon mauritianum* | ant | Formicidae spp. | | | x | |
| *Senegalia brevispica* | ant | Formicidae spp. | | x | x | |
| *Vachellia gerrardii* | ant | Formicidae spp. | | | x | |
| *Balanites* sp. | ant | Formicidae spp. | | | x | x |
| *Gutenbergia cordifolia* | ant | Formicidae spp. | | x | | |
| *Hibiscus vitifolius* | ant | Formicidae spp. | | x | x | |
| *Indigofera volkensii* | ant | Formicidae spp. | | | x | x |
| *Lippia kituiensis* | ant | Formicidae spp. | x | | | |
| *Melhania ovata* | ant | Formicidae spp. | | | x | |
| *Ocimum forskolei* | ant | Formicidae spp. | | x | x | |
| *Pentanisia ouranogyne* | ant | Formicidae spp. | | x | | |
| *Abutilon mauritianum* | bug | unknown Hemiptera sp. | | | x | |
| *Hibiscus flavifolius* | beetle | ?Alticinae sp. 1 | | x | | |
| *Ipomoea sinensis* | beetle | ?Alticinae sp. 1 | | x | | |
| *Lippia kituiensis* | beetle | ?Alticinae sp. 1 | x | x | | |
| *Croton dichogamous* | beetle | Alticinae sp. 1 | | | | x |
| *Helichrysum glumaceum* | beetle | Alticinae sp. 1 | | x | | |
| *Lippia kituiensis* | beetle | Alticinae sp. 1 | | x | | |
| *Senegalia brevispica* | beetle | ?*Megalognatha meruensis* | | | | x |
| *Vachellia gerrardii* | beetle | ?*Megalognatha meruensis* | | x | | |
| *Vachellia gerrardii* | beetle | Galerucinae sp. 11 | | x | | |
| *Croton dichogamous* | beetle | Galerucinae sp. 6 | | | | x |
| *Croton dichogamous* | beetle | Clytrinae sp. 1 | | x | | |
| *Hibiscus vitifolius* | beetle | Chrysomelidae sp. 1 | | | x | |
| *Gutenbergia cordifolia* | beetle | *Coryna* ?*ambigua* | | x | | |
| *Melhania ovata* | beetle | *Coryna* ?*ambigua* | | | x | |
| *Hibiscus vitifolius* | beetle | *Coryna* ?*chevrolati* | | | x | |
| *Helichrysum glumaceum* | beetle | unknown *Coryna* spp. | | x | | |
| *Ipomoea sinensis* | beetle | unknown *Coryna* spp. | | x | | |
| *Croton dichogamous* | beetle | Cerambycidae sp. 1 | | | x | |
| *Felicia muricola* | beetle | Cerambycidae sp. 2 | | | x | |
| *Hibiscus vitifolius* | beetle | Curculionidae sp. | | x | x | |
| *Senegalia brevispica* | beetle | *Idgia* sp. | | | x | |
| *Felicia muricola* | beetle | *Lycus serenus* | | | | x |
| *Lippia kituiensis* | beetle | *Lycus serenus* | | x | | |
| *Croton dichogamous* | beetle | *Lycus* sp. 1 | | | | x |
| *Gutenbergia cordifolia* | beetle | *Rhabdotis sobrina* | | x | | |

| **Plant species** | **Visitor species** | | **TP1** | **TP2** | **TP3** | **TP4** |
|---|---|---|---|---|---|---|
| *Senegalia brevispica* | moth | Arctiidae sp. | | | | x |
| *Vachellia gerrardii* | moth | Arctiidae sp. | | | | x |
| *Lippia kituiensis* | moth | Arctiidae sp. | | | | x |
| *Hibiscus flavifolius* | moth | *Cephanodes hylas* | | x | | |
| *Senegalia brevispica* | b'fly | Lycaenidae spp. | | | | x |
| *Vachellia gerrardii* | b'fly | Lycaenidae spp. | | | | x |
| *Indigofera volkensii* | b'fly | Lycaenidae spp. | | | x | |
| *Ocimum forskolei* | b'fly | Lycaenidae spp. | | | x | |
| *Priva curtisiae* | b'fly | Lycaenidae spp. | | | x | |
| *Hibiscus flavifolius* | b'fly | Pieridae spp. | | | x | |
| *Hibiscus aponeurus* | b'fly | *Saragnesa phidyle* | | | | x |
| *Pentanisia ouranogyne* | b'fly | *Spiralia* sp. | | | | x |
| *Senegalia brevispica* | b'fly | unknown butterfly spp. | | | x | |
| *Melhania ovata* | b'fly | unknown butterfly spp. | | | x | |
| *Felicia muricola* | moth | unknown moth sp. | | | | x |

(b) Turkana Boma, June

| **Plant species** | **Visitor species** | | **TP1** | **TP2** | **TP3** | **TP4** |
|---|---|---|---|---|---|---|
| *Abutilon mauritianum* | bee | *Apis mellifera* | | x | | |
| *Lippia kituiensis* | bee | *Apis mellifera* | | | | x |
| *Monechma* sp. B | bee | *Apis mellifera* | | x | x | |
| *Gutenbergia cordifolia* | bee | *Plebeina hildebrantii* | | | x | |
| *Justicia lorata* | bee | *Plebeina hildebrantii* | | | x | |
| *Ipomoea ficifolia* | bee | *Hypotrigona ruspolii* | | | x | |
| *Justicia diclipteroides* | bee | *Amegilla calens* | | x | | |
| *Abutilon mauritianum* | bee | large Apidae spp. | | x | | |
| *Leucas glabrata* | bee | large Apidae spp. | | x | x | x |
| *Monechma* sp. B | bee | large Apidae spp. | | x | x | x |
| *Polygala sphenoptera* | bee | large Apidae spp. | | x | x | |
| *Gutenbergia cordifolia* | bee | *Ceratina moerenhouti* | | | | x |
| *Plectranthus caninus* | bee | *Ceratina nyassensis* | | | x | |
| *Ipomoea sinensis* | bee | *Macrogalea candida* | | x | x | |
| *Senegalia brevispica* | bee | *Hylaeus* sp. b | | | x | |
| *Justicia lorata* | bee | *?Hylaeus* sp. | | x | | |
| *Abutilon mauritianum* | bee | *Lipotriches (Lipotriches)* sp. 1 | | x | | |
| *Senegalia brevispica* | bee | *Lipotriches (Lipotriches)* sp. 1 | | | x | |
| *Gutenbergia cordifolia* | bee | *Lipotriches (Lipotriches)* sp. 1 | | x | x | |
| *Senegalia brevispica* | bee | *Lipotriches (Lipotriches)* sp. A | | | x | |
| *Abutilon mauritianum* | bee | *Lipotriches (Lipotriches)* sp. H | | | x | |
| *Gutenbergia cordifolia* | bee | *Halictus (Seladonia)* sp. 1 | | x | | |
| *?Becium* sp. | bee | *Halictus (Seladonia)* sp. 2 | | x | | |
| *Justicia lorata* | bee | *Halictus (Seladonia)* sp. 2 | | x | x | |
| *Abutilon mauritianum* | bee | *Halictus (Seladonia)* sp. C | | | x | |
| *Gutenbergia cordifolia* | bee | *Halictus (Seladonia)* sp. C | | | x | |
| *Ipomoea obscura* | bee | *Halictus (Seladonia)* sp. C | | | | x |
| *Sida ovata* | bee | *Halictus (Seladonia)* sp. C | | | x | |
| *Hibiscus flavifolius* | bee | *Lasioglossum (Dialictus)* sp. 2 | | | x | |
| *Plectranthus caninus* | bee | *Lasioglossum (Dialictus)* sp. 2 | | x | | |

| **Plant species** | **Visitor species** | | **TP1** | **TP2** | **TP3** | **TP4** |
|---|---|---|---|---|---|---|
| *Justicia diclipteroides* | bee | *Lasioglossum* sp. B | | x | | x |
| *Hibiscus vitifolius* | bee | *Patellapis* sp. A | | x | | |
| *Ipomoea ficifolia* | bee | *Patellapis* sp. A | | x | | |
| *Ipomoea obscura* | bee | *Patellapis* sp. C | | x | | |
| *Barleria spinisepala* | bee | unknown Halictidae sp. | | | x | |
| *Gutenbergia cordifolia* | bee | *Megachile (Chalicodoma)* sp. 2 | | | | x |
| *Monechma* sp. B | bee | *Megachile (Chalicodoma)* sp. 2 | | x | | |
| *Gutenbergia cordifolia* | bee | *Megachile (Chalicodoma) sp. small* | | | | x |
| *Gutenbergia cordifolia* | bee | *Megachile (Pseudomegachile)* sp. 1 | | | | x |
| *Justicia diclipteroides* | bee | *Megachile (Pseudomegachile)* sp. 1 | | x | | |
| *Ocimum forskolei* | bee | *Heriades (Heriades)* sp. 1 | | x | x | |
| *Plectranthus caninus* | bee | *Heriades (Heriades)* sp. 1 | | x | | |
| *Gutenbergia cordifolia* | bee | *Heriades* sp. a | | x | x | |
| *?Becium* sp. | bee | Osmiini sp. a | | | x | |
| *Abutilon mauritianum* | bee | small bee sp. | | | x | |
| *Abutilon mauritianum* | bee | med bee spp. | | x | x | |
| *Senegalia brevispica* | bee | med bee spp. | | | x | |
| *Evolvulus alsinoides* | bee | med bee spp. | | | x | |
| *Gutenbergia cordifolia* | bee | med bee spp. | | x | x | |
| *Ipomoea ficifolia* | bee | med bee spp. | | x | | |
| *Helichrysum glumaceum* | bee | unknown bee spp. | | | | x |
| *Helichrysum glumaceum* | wasp | Chrysididae sp. | | x | | |
| *Aerva lanata* | wasp | Chrysididae spp. | | | x | |
| *Aerva lanata* | wasp | Chrysididae spp. | | | x | x |
| *Monechma* sp. B | wasp | Eumenidae sp. 13 | | x | | |
| *Senegalia brevispica* | wasp | Eumenidae sp. 14 | | x | | |
| *Monechma* sp. B | wasp | Eumenidae sp. 3 | | | x | |
| *Helichrysum glumaceum* | wasp | Eumenidae sp. 8 | | | x | |
| *Helichrysum glumaceum* | wasp | *Cerceris* sp. 2 | | | | x |
| *Justicia lorata* | wasp | *Tachysphex* sp. 1 | | | x | |
| *Cyphostemma serpens* | wasp | *Tachytes* sp. 1 | | x | x | |
| *Aerva lanata* | wasp | wasp sp. 2 | | | x | |
| *Senegalia brevispica* | wasp | unknown wasp sp. | | x | | |
| *Gutenbergia cordifolia* | fly | *Chloropidae* sp. 1 | x | | | |
| *Justicia diclipteroides* | fly | *Coenosia exigua* | | | x | |
| *Senegalia brevispica* | fly | *Limnophora quaterna* | | x | | |
| *Helichrysum glumaceum* | fly | Culicidae spp. | | | x | |
| *Cyphostemma serpens* | fly | *Eumerus obliquus* | | x | | |
| *Helichrysum glumaceum* | fly | *Gonarthrus* sp. 1 | | x | | |
| *Aerva lanata* | fly | tiny Diptera sp. | | | | x |
| *?Becium* sp. | ant | Formicidae spp. | | x | | |
| *Abutilon mauritianum* | ant | Formicidae spp. | | x | | |
| *Barleria spinisepala* | ant | Formicidae spp. | | | x | |
| *Euphorbia sp.* | ant | Formicidae spp. | | | x | |
| *Hibiscus vitifolius* | ant | Formicidae spp. | | x | | |
| *Indigofera volkensii* | ant | Formicidae spp. | | x | x | |
| *Ipomoea obscura* | ant | Formicidae spp. | | | | x |
| *Justicia diclipteroides* | ant | Formicidae spp. | | x | | |
| *Lippia kituiensis* | ant | Formicidae spp. | | | x | |
| *Aerva lanata* | beetle | Bruchidae sp. | | x | x | x |

| Plant species | Visitor species | | TP1 | TP2 | TP3 | TP4 |
|---|---|---|---|---|---|---|
| *Ipomoea ficifolia* | beetle | Bruchidae spp. | | | x | |
| *Senegalia brevispica* | beetle | Cerambycidae sp. 1 | | x | | |
| *Ipomoea ficifolia* | beetle | Alticinae sp. 1 | | x | | |
| *Vachellia nilotica* | beetle | Alticinae sp. 2 | | x | | |
| *Vachellia nilotica* | beetle | Clytrinae sp. 3 | | x | | |
| *Hibiscus vitifolius* | beetle | Clytrinae sp. 5 | | x | | |
| *Senegalia brevispica* | beetle | Galerucinae sp. 5 | | x | | |
| *Senegalia brevispica* | beetle | *Megalognatha meruensis* | | | x | |
| *Hibiscus aponeurus* | beetle | *Coryna ?apicornis* | | x | x | |
| *Hibiscus flavifolius* | beetle | *Coryna ?apicornis* | | x | | |
| *Hibiscus vitifolius* | beetle | *Coryna ?apicornis* | | | x | |
| *Ipomoea ficifolia* | beetle | *Coryna ?apicornis* | | | x | |
| *Hibiscus aponeurus* | beetle | unknown *Coryna* sp. | | | x | |
| *Senegalia brevispica* | beetle | *Lycus serenus* | | x | | |
| *Helichrysum glumaceum* | b'fly | *Anthene amarah amarah* | | x | | |
| *Gutenbergia cordifolia* | b'fly | *Eicochrysops masai* | | | x | |
| *Senegalia brevispica* | b'fly | Lycaenidae sp. | | x | | |
| *Gutenbergia cordifolia* | b'fly | Lycaenidae sp. | | | x | x |
| *Indigofera volkensii* | b'fly | *Freyeria trochylus trochylus* | | | x | |
| *Gutenbergia cordifolia* | b'fly | Pieridae spp. | | | x | |
| *Hibiscus flavifolius* | b'fly | Pieridae spp. | | | x | |
| *Monechma* sp. B | b'fly | *Sarangesa phidyle* | | | | x |
| *Evolvulus alsinoides* | b'fly | unknown butterfly sp. | | x | | |
| *Gutenbergia cordifolia* | b'fly | unknown butterfly spp. | | | | x |
| *Hibiscus aponeurus* | b'fly | unknown butterfly spp. | | | x | |
| *Kalanchoe* sp. 1 | b'fly | unknown butterfly spp. | | | x | |

(c) Turkana Boma, July

| Plant species | Visitor species | | TP1 | TP2 | TP3 | TP4 |
|---|---|---|---|---|---|---|
| *Barleria spinisepala* | bee | *Apis mellifera* | | x | | |
| *Abutilon mauritianum* | bee | *Ceratina nyassensis* | | | x | |
| *Barleria spinisepala* | bee | *Ceratina nyassensis* | | | x | |
| *Ipomoea sinensis* | bee | *Ceratina nyassensis* | | | x | |
| *Abutilon mauritianum* | bee | *Hylaeus sp.* | | | x | |
| *Senegalia brevispica* | bee | *Pseudapis (Pseudapis)* sp. 1 | | | x | |
| *Senegalia brevispica* | bee | Osmiini sp. d | | | x | |
| *Commelina* spp. blue | | unknown small black bee/fly | | x | | |
| *Senegalia brevispica* | wasp | *Eumenidae* sp. 4 | | | x | |
| *Senegalia brevispica* | wasp | *Tachysphex* sp. 1 | | | x | |
| *Senegalia brevispica* | wasp | *?Tachysphex* sp. 1 | | | x | |
| *Senegalia brevispica* | fly | *Rhyncomya* spp. | x | | | |
| *Commelina* spp. blue | fly | *Rhyncomya* spp. | | | x | |
| *Osteospermum vaillantii* | fly | Tephritidae sp. 1 | | | x | |
| *Senegalia brevispica* | fly | Diptera sp. | | | x | |
| *Vachellia nilotica* | ant | Formicidae spp. | | | x | |
| *Barleria spinisepala* | ant | Formicidae spp. | | x | x | |
| *Polygala sphenoptera* | ant | Formicidae spp. | | | | x |
| *Senegalia brevispica* | bug | Hemiptera spp. (juvenile) | | | | x |

| Plant species | Visitor species | | TP1 | TP2 | TP3 | TP4 |
|---|---|---|---|---|---|---|
| *Pavonia gallaensis* | bug | Hemiptera spp. (juvenile) | | x | | |
| *Abutilon mauritianum* | beetle | Buprestidae sp. 1 | | | x | |
| *Abutilon mauritianum* | *beetle* | *Coryna ?ambigua* | | | x | |

(d) Turkana Boma, August

| Plant species | Visitor species | | TP1 | TP2 | TP3 | TP4 |
|---|---|---|---|---|---|---|
| *Senegalia brevispica* | bee | *Apis mellifera* | | | x | x |
| *Vachellia etbaica* | bee | *Apis mellifera* | | x | x | x |
| *Commelina* spp. blue | bee | *Apis mellifera* | | x | | |
| *Leucas glabrata* | bee | *Apis mellifera* | | x | | |
| *Sida schimperiana* | bee | *Apis mellifera* | | x | | |
| *Senegalia brevispica* | bee | *Plebeina hildebrantii* | | x | x | |
| *Euphorbia* sp. | bee | *Plebeina hildebrantii* | | | x | |
| *Phyllanthus sepialis* | bee | *Plebeina hildebrantii* | | x | | |
| *Solanum sp. 1* | bee | *Plebeina hildebrantii* | | | x | |
| *Commelina* spp. blue | bee | *Amegilla penicula* | | x | | |
| *Leucas glabrata* | bee | large Apidae sp. | | x | | |
| *Gutenbergia cordifolia* | bee | *Ceratina nyassensis* | | | x | |
| *Vachellia etbaica* | bee | *Xylocopa somalica* | | | x | |
| *Leucas glabrata* | bee | *Xylocopa somalica* | | x | x | |
| *Solanum* sp. 1 | bee | *Xylocopa somalica* | | x | | |
| *Euphorbia sp.* | bee | *Pseudapis (Pseudapis)* sp. 1 | | | x | |
| *Solanum* sp. 1 | bee | *Lipotriches (Lipotriches)* sp. 1 | | x | | |
| *Lippia kituiensis* | bee | *Patellapis (Zonalictus)* sp. 1 | | x | | |
| *Gutenbergia cordifolia* | bee | *Patellapis* sp. C | | | x | |
| *Polygala sphenoptera* | bee | *Patellapis* sp. C | x | x | | |
| *Senegalia brevispica* | bee | unknown Halictidae sp. | | x | | |
| *Monechma* sp. B | bee | *Megachile (Chalicodoma)* sp. 2 | | | | x |
| *Aerva lanata* | wasp | *Chrysididae* sp. | | | x | |
| *Phyllanthus sepialis* | wasp | *Ichneumonidae* sp. | | | | x |
| *Phyllanthus sepialis* | wasp | *Cerceris* sp. 2 | | | x | |
| *Ipomoea sinensis* | wasp | *Liris* sp. 1 | | | x | |
| *Phyllanthus sepialis* | wasp | wasp sp. 1 | | x | | |
| *Justicia lorata* | wasp | unknown wasp sp. | | | x | |
| *Lippia kituiensis* | fly | *Bombomyia discoidea* | | x | | |
| *Justicia lorata* | fly | Bombyliidae sp. | | | x | |
| *Lippia kituiensis* | fly | *Rhyncomya* sp. | x | | | |
| *Euphorbia* sp. | fly | Miltogramminae sp. | | | x | |
| *Senegalia brevispica* | fly | unknown Diptera spp. | x | | x | |
| *Vachellia etbaica* | fly | unknown Diptera spp. | | | x | |
| *Vachellia etbaica* | ant | Formicidae spp. | | | x | x |
| *Aerva lanata* | ant | Formicidae spp. | | | x | x |
| *Barleria spinisepala* | ant | Formicidae spp. | | | | x |
| *Emilia discifolia* | ant | Formicidae spp. | | | | x |
| *Euphorbia* sp. | ant | Formicidae spp. | | | x | |
| *Hibiscus aponeurus* | ant | Formicidae spp. | | x | | |
| *Monechma* sp. B | ant | Formicidae spp. | | | x | x |
| *Ocimum forskolei* | ant | Formicidae spp. | | x | x | x |

| Plant species | Visitor species | | TP1 | TP2 | TP3 | TP4 |
|---|---|---|---|---|---|---|
| *Ruellia sp.* | ant | Formicidae spp. | | x | | |
| *Aerva lanata* | bug | Hemiptera sp. | | | x | |
| *Senegalia brevispica* | b'fly | Pieridae spp. | | | x | |
| *Hibiscus aponeurus* | b'fly | Pieridae spp. | | x | | |

(e) Junction, June

| Plant species | Visitor species | | TP1 | TP2 | TP3 | TP4 |
|---|---|---|---|---|---|---|
| *Emilia discifolia* | bee | *Apis mellifera* | | | x | |
| *Hypoestes forskahlii* | bee | *Apis mellifera* | | | x | |
| *Ipomoea kituiensis* | bee | *Apis mellifera* | | x | | |
| *Leucas glabrata* | bee | *Apis mellifera* | | | | x |
| *Monechma* sp. B | bee | *Apis mellifera* | | x | | x |
| *Leucas glabrata* | bee | *Amegilla calens* | x | | | |
| *Solanum* sp. 1 | bee | *Amegilla calens* | | x | | |
| *Polygala* sp. 2 | bee | *Amegilla capensis* | | x | | |
| *Echiochilon lithospermoides* | bee | *Amegilla penicula* | | | | x |
| *Solanum* sp. 1 | bee | *Amegilla penicula* | | x | | |
| *Gutenbergia cordifolia* | bee | *Anthophora pygmaea* | | | x | |
| *Senegalia brevispica* | bee | large Apidae spp. | | | x | |
| *Barleria spinisepala* | bee | large Apidae spp. | | x | | |
| *Cassia mimosoides* | bee | large Apidae spp. | x | | | |
| *Gutenbergia cordifolia* | bee | large Apidae spp. | | | x | |
| *Hypoestes forskahlii* | bee | large Apidae spp. | | x | x | x |
| *Leucas glabrata* | bee | large Apidae spp. | | | x | |
| *Lippia kituiensis* | bee | large Apidae spp. | | | x | |
| *Ipomoea kituiensis* | bee | *Tetralonia nigropilosa* | | x | | |
| *Monechma* sp. B | bee | *Thyreus calceatus* | | | x | |
| *Leucas glabrata* | bee | *Xylocopa somalica* | | | | x |
| *Heliotropium steudneri* | bee | *Ceratina moerenhouti* | | | x | |
| *Monechma* sp. B | bee | *Ceratina moerenhouti* | | | x | |
| *Ipomoea hildebrantii* | bee | *Colletes* sp. 2 | | | x | |
| *Solanum* sp. 1 | bee | *Lipotriches (Lipotriches)* sp. C | | x | | |
| *Monechma* sp. B | bee | *Lipotriches (Lipotriches)* sp. G | | | x | |
| *Monechma* sp. B | bee | *Lipotriches (Lipotriches)* sp. H | | | x | |
| *Senegalia brevispica* | bee | *Lipotriches (Lipotriches)* sp. M | | x | | |
| *Solanum* sp. 1 | bee | *Lipotriches* sp. A | | x | | |
| *Solanum* sp. 1 | bee | *?Lipotriches* sp. 1 | | x | | |
| *Endostemon tereticaulis* | bee | *Pseudapis (Pseudapis)* sp. 1 | | | x | |
| *Helichrysum glumaceum* | bee | *Pseudapis (Pseudapis)* sp. 1 | | | x | |
| *Solanum* sp. 1 | bee | *Pseudapis (Pseudapis)* sp. 1 | | | x | |
| *Ipomoea kituiensis* | bee | *Patellapis* sp. A | x | | | |
| *Monechma* sp. B | bee | *Patellapis* sp. A | | | x | |
| *Evolvulus alsinoides* | bee | *Halictus (Seladonia)* sp. 1 | | | x | |
| *Ipomoea kituiensis* | bee | *Systropha* sp. 1 | | x | | |
| *Hypoestes forskahlii* | bee | Halictidae sp. 3 | | | x | |
| *Gutenbergia cordifolia* | bee | Halictidae sp. 4 | | | x | |
| *Gutenbergia cordifolia* | bee | *Megachile (Chalicodoma)* spp. | | | x | |
| *Monechma* sp. B | bee | *Heriades (Heriades)* sp. 1 | | x | | |

| **Plant species** | **Visitor species** | | **TP1** | **TP2** | **TP3** | **TP4** |
|---|---|---|---|---|---|---|
| *Ocimum forskolei* | bee | *Heriades (Heriades)* sp. 1 | | | | x |
| *Plectranthus caninus* | bee | *Heriades (Heriades)* sp. 1 | | x | | |
| *Gutenbergia cordifolia* | bee | Heriades sp. a | | | | x |
| *Gutenbergia cordifolia* | bee | Osmiini sp. e | | | x | |
| *Justicia lorata* | bee | Osmiini sp. e | | | x | |
| *Monechma* sp. B | bee | Osmiini sp. e | | | x | |
| *Ipomoea hildebrantii* | bee | unknown Osmiini sp. | | | x | |
| *Gutenbergia cordifolia* | bee | ?*Aspidosmia* sp. 1 | | | | x |
| *Monechma* sp. B | bee | ?*Ichteranthidium* sp. 1 | | | x | |
| *Heliotropium steudneri* | bee | Anthidiini sp. 1 | | | x | |
| *Gutenbergia cordifolia* | bee | med bee spp. | | | x | |
| *Ipomoea hildebrantii* | bee | med bee spp. | | x | | |
| *Ipomoea sinensis* | bee | med bee spp. | | | x | |
| *Endostemon tereticaulis* | bee | small bee spp. | | | x | |
| *Justicia lorata* | bee | small bee spp. | | | x | |
| *Gutenbergia cordifolia* | bee | unknown bee spp. | | | | x |
| *Gutenbergia cordifolia* | bee | unknown bee spp. | | x | | |
| *Ipomoea sinensis* | bee | unknown bee spp. | | x | | |
| *Ipomoea sinensis* | bee | unknown bee spp. | | | x | |
| *Helichrysum glumaceum* | wasp | Chrysididae sp. | | x | | |
| *Senegalia brevispica* | wasp | Eumenidae sp. 15 | | | x | |
| *Monechma* sp. B | wasp | Eumenidae sp. 16 | | | x | |
| *Helichrysum glumaceum* | wasp | Eumenidae sp. 8 | | | x | x |
| *Monechma* sp. B | wasp | Eumenidae sp. 9 | | | x | |
| *Heliotropium steudneri* | wasp | *Ammophila* sp. 1 | | | x | |
| *Leucas glabrata* | wasp | *Ammophila* sp. 1 | | x | | |
| *Helichrysum glumaceum* | wasp | *Philanthus* sp. 3 | | | x | |
| *Tagetes minuta* | wasp | Pompilidae sp. 2 | | | x | |
| *Monechma* sp. B | wasp | ?*Polistes* sp. | | x | | |
| *Senegalia brevispica* | wasp | unknown wasp spp. | | | x | |
| *Emilia discifolia* | wasp | unknown wasp spp. | | x | | |
| *Leucas glabrata* | wasp | unknown wasp spp. | | | | x |
| *Justicia lorata* | fly | Bombyliidae sp. | | x | | |
| *Euclea* sp. | fly | *Coenosia cuthbertsoni* | | x | | |
| *Justicia lorata* | fly | Syrphidae sp. | | | x | |
| *Emilia discifolia* | fly | Tephritidae sp. | | | x | |
| *Euclea* sp. | fly | unknown Diptera spp. | x | | | |
| *Helichrysum glumaceum* | fly | unknown Diptera spp. | | x | | |
| *Solanum* sp. 1 | fly | unknown Diptera spp. | | | | x |
| ?*Becium* sp. | ant | Formicidae spp. | | | x | |
| *Senegalia brevispica* | ant | Formicidae spp. | | x | | |
| *Barleria spinisepala* | ant | Formicidae spp. | | | x | |
| *Cassia mimosoides* | ant | Formicidae spp. | | | x | |
| *Euclea* sp. | ant | Formicidae spp. | x | x | x | x |
| *Heliotropium steudneri* | ant | Formicidae spp. | | | x | |
| *Leucas glabrata* | ant | Formicidae spp. | | | | x |
| *Sida ovata* | beetle | Alticinae sp. 1 | | x | | |
| *Solanum* sp. 1 | beetle | Alticinae sp. 1 | | | x | |
| *Senegalia brevispica* | beetle | *Megalognatha meruensis* | | x | | |
| *Cassia mimosoides* | beetle | Clytrinae sp. 4 | | x | | |

| Plant species | Visitor species | | TP1 | TP2 | TP3 | TP4 |
|---|---|---|---|---|---|---|
| *Ipomoea hildebrantii* | beetle | *Coryna ?chevrolati* | | x | x | |
| *Tagetes minuta* | beetle | *Idgia* sp. | | | x | |
| *Pavonia gallaensis* | beetle | Lamiinae sp.1 | | | x | |
| *Emilia discifolia* | beetle | Phalacridae sp. | | | x | |
| *Sida ovata* | beetle | unknown Coleoptera sp. | | | x | |
| *Senegalia brevispica* | b'fly | *Azanus jesous* | | | x | |
| *Senegalia brevispica* | b'fly | Lycaenidae sp. | | | | x |
| *Emilia discifolia* | b'fly | *Eurema brigitta brigitta* | | | | x |
| *Heliotropium steudneri* | b'fly | *Freyeria trochylus trochylus* | | | x | |
| *Leucas glabrata* | b'fly | Pieridae sp. | | x | | |

(f) Junction, July

| Plant species | Visitor species | | TP1 | TP2 | TP3 | TP4 |
|---|---|---|---|---|---|---|
| *Hypoestes forskahlii* | bee | *Amegilla penicula* | | x | | |
| *Hypoestes forskahlii* | bee | large Apidae sp. | | | x | |
| *Pavonia gallaensis* | bee | *Ceratina nyassensis* | | | x | |
| *Osteospermum vaillantii* | bee | *Halictus (Seladonia)* sp. 1 | | | x | |
| *Pavonia gallaensis* | bee | *Lasioglossum (Dialictus)* sp. 1 | | x | | |
| *Senegalia brevispica* | bee | *Pseudapis (Pseudapis)* sp. 1 | | | x | |
| *Osteospermum vaillantii* | bee | unknown Halictidae sp. | | | x | |
| *Pavonia gallaensis* | bee | Osmiini sp. j | | x | | |
| *Emilia discifolia* | bee | small green bee spp. | | | x | x |
| *Osteospermum vaillantii* | bee | med bee sp. | | | x | |
| *Evolvulus alsinoides* | bee | small bee spp. | | x | | |
| *Pavonia gallaensis* | bee | small bee spp. | | x | | |
| *Senegalia brevispica* | bee | small bee spp. | | | x | |
| *Ipomoea sinensis* | bee | unknown bee sp. | | | x | |
| *Hypoestes forskahlii* | wasp | Eumenidae sp. 9 | | x | | |
| *Monechma* sp. B | wasp | Eumenidae sp. 9 | | | | x |
| *Senegalia brevispica* | wasp | *Cathimeris* sp. | | | x | |
| *Senegalia brevispica* | wasp | *Cerceris* sp. 2 | | x | x | |
| *Monechma* sp. B | wasp | Sphecidae sp. | | x | | |
| *Osteospermum vaillantii* | wasp | unknown wasp spp. | | | x | |
| *Senegalia brevispica* | wasp | unknown wasp spp. | | | x | |
| *Senegalia brevispica* | fly | *Rhyncomya* sp. | | x | | |
| *Senegalia brevispica* | b'fly | *Hoplacephala inermis* | x | x | | |
| *Senegalia brevispica* | b'fly | *Belenois aurota aurota* | | x | | |
| *Echiochilon lithospermoides* | b'fly | *Eurema brigitta brigitta* | | | x | |
| *Hypoestes forskahlii* | b'fly | *Spialia mata higginsi* | | x | | |

Appendix 10. Summary of the number of visitor types, interaction types and interaction frequencies in each seasonal web by time period and visitor group. Total visits, plant species observed and plant species visited are also shown for each time period.

(a) Turkana Boma, May

| | TP 1 | TP 2 | TP 3 | TP 4 | Overall |
|---|---|---|---|---|---|
| Total visits | 64 | 291 | 172 | 306 | **833** |
| Plant species observed | 30 | 38 | 34 | 23 | **38** |
| Plant species visited | 8 | 29 | 21 | 11 | **33** |
| **Visitor types** | | | | | |
| bees | 3 | 17 | 20 | 4 | **33** |
| wasps | 0 | 3 | 3 | 3 | **6** |
| ants | 1 | 1 | 1 | 1 | **1** |
| flies | 5 | 14 | 10 | 2 | **18** |
| bugs | 0 | 0 | 1 | 0 | **1** |
| beetles | 1 | 10 | 7 | 5 | **17** |
| butterflies and moths | 0 | 1 | 3 | 5 | **8** |
| **Total** | **10** | **45** | **45** | **20** | **84** |
| **Interaction types** | | | | | |
| bees | 4 | 36 | 28 | 6 | **67** |
| wasps | 0 | 3 | 3 | 3 | **8** |
| ants | 1 | 5 | 8 | 2 | **11** |
| flies | 6 | 22 | 13 | 3 | **33** |
| bugs | 0 | 0 | 1 | 0 | **1** |
| beetles | 1 | 14 | 7 | 5 | **25** |
| butterflies and moths | 0 | 1 | 6 | 8 | **15** |
| **Total** | **12** | **81** | **66** | **27** | **160** |
| **Visits** | | | | | |
| bees | 479 | 48 | 138 | 107 | **186** |
| wasps | 19 | 0 | 5 | 3 | **11** |
| ants | 41 | 4 | 21 | 14 | **2** |
| flies | 132 | 11 | 89 | 25 | **7** |
| bugs | 1 | 0 | 0 | 1 | **0** |
| beetles | 59 | 1 | 35 | 15 | **8** |
| butterflies and moths | 102 | 0 | 3 | 7 | **92** |
| **Total** | **833** | **64** | **291** | **172** | **306** |
| **Interaction frequency** | | | | | |
| bees | 4111 | 5794 | 12306 | 13152 | **35363** |
| wasps | 0 | 266 | 230 | 839 | **1335** |
| ants | 233 | 2421 | 631 | 372 | **3657** |
| flies | 998 | 7172 | 2342 | 437 | **10949** |
| bugs | 0 | 0 | 92 | 0 | **92** |
| beetles | 58 | 1301 | 585 | 191 | **2135** |
| butterflies and moths | 0 | 5 | 375 | 7722 | **8102** |
| **Total** | **5400** | **16959** | **16561** | **22713** | **61633** |

(b) Turkana Boma, June

| | TP 1 | TP 2 | TP 3 | TP 4 | Overall |
|---|---|---|---|---|---|
| Total visits | 1 | 133 | 206 | 55 | **395** |
| Plant species observed | 23 | 31 | 32 | 23 | **32** |
| Plant species visited | 1 | 24 | 26 | 8 | **28** |
| | | | | | |
| **Visitor types** | | | | | |
| bees | 0 | 17 | 19 | 9 | **30** |
| wasps | 0 | 5 | 6 | 2 | **10** |
| ants | 0 | 1 | 1 | 1 | **1** |
| flies | 1 | 3 | 2 | 1 | **7** |
| beetles | 0 | 9 | 4 | 1 | **11** |
| butterflies and moths | 0 | 3 | 5 | 3 | **7** |
| **Total** | **1** | **38** | **37** | **17** | **66** |
| | | | | | |
| **Interaction types** | | | | | |
| bees | 0 | 27 | 28 | 10 | **51** |
| wasps | 0 | 5 | 7 | 2 | **11** |
| ants | 0 | 5 | 4 | 1 | **9** |
| flies | 1 | 3 | 2 | 1 | **7** |
| beetles | 0 | 10 | 7 | 1 | **15** |
| butterflies and moths | 0 | 3 | 7 | 3 | **12** |
| **Total** | **1** | **53** | **55** | **18** | **105** |
| | | | | | |
| **Visits** | | | | | |
| bees | 181 | 0 | 77 | 78 | **26** |
| wasps | 76 | 0 | 12 | 50 | **14** |
| ants | 23 | 0 | 15 | 7 | **1** |
| flies | 14 | 1 | 5 | 7 | **1** |
| beetles | 55 | 0 | 17 | 32 | **6** |
| butterflies and moths | 46 | 0 | 7 | 32 | **7** |
| **Total** | **395** | **1** | **133** | **206** | **55** |
| | | | | | |
| **Interaction frequency** | | | | | |
| bees | 0 | 3902 | 3552 | 1957 | **9202** |
| wasps | 0 | 167 | 382 | 45 | **535** |
| ants | 0 | 102 | 120 | 3 | **216** |
| flies | 63 | 35 | 24 | 2 | **124** |
| beetles | 0 | 163 | 103 | 10 | **260** |
| butterflies and moths | 0 | 37 | 463 | 876 | **769** |
| **Total** | **63** | **4406** | **4644** | **2684** | **11797** |

(c) Turkana Boma, July

| | **TP 1** | **TP 2** | **TP 3** | **TP 4** | **Overall** |
|---|---|---|---|---|---|
| Total visits | 4 | 9 | 39 | 2 | **54** |
| Plant species observed | 6 | 9 | 9 | 6 | **10** |
| Plant species visited | 1 | 3 | 7 | 2 | **9** |
| | | | | | |
| **Visitor types** | | | | | |
| bees | 0 | 2 | 4 | 0 | **6** |
| wasps | 0 | 0 | 3 | 0 | **3** |
| ants | 0 | 1 | 1 | 1 | **1** |
| flies | 1 | 0 | 3 | 0 | **3** |
| beetles | 0 | 0 | 2 | 0 | **2** |
| bugs | 0 | 1 | 0 | 1 | **1** |
| Total | 1 | 4 | 13 | 2 | **16** |
| | | | | | |
| **Interaction types** | | | | | |
| bees | 0 | 2 | 6 | 0 | **8** |
| wasps | 0 | 0 | 3 | 0 | **3** |
| ants | 0 | 1 | 2 | 1 | **3** |
| flies | 1 | 0 | 3 | 0 | **4** |
| beetles | 0 | 0 | 2 | 0 | **2** |
| bugs | 0 | 1 | 0 | 1 | **2** |
| **Total** | **1** | **4** | **16** | **2** | **22** |
| | | | | | |
| **Visits** | | | | | |
| bees | 16 | 0 | 3 | 13 | **0** |
| wasps | 16 | 0 | 0 | 16 | **0** |
| ants | 10 | 0 | 5 | 4 | **1** |
| flies | 8 | 4 | 0 | 4 | **0** |
| beetles | 2 | 0 | 0 | 2 | **0** |
| bugs | 2 | 0 | 1 | 0 | **1** |
| **Total** | **54** | **4** | **9** | **39** | **2** |
| | | | | | |
| **Interaction frequency** | | | | | |
| bees | 0 | 49 | 466 | 0 | **515** |
| wasps | 0 | 0 | 1644 | 0 | **1644** |
| ants | 0 | 195 | 50 | 2 | **247** |
| flies | 371 | 0 | 208 | 0 | **579** |
| beetles | 0 | 0 | 8 | 0 | **8** |
| bugs | 0 | 2 | 0 | 74 | **76** |
| **Total** | **371** | **246** | **2376** | **76** | **3069** |

(d) Turkana Boma, August

| | **TP 1** | **TP 2** | **TP 3** | **TP 4** | **Overall** |
|---|---|---|---|---|---|
| Total visits | 8 | 112 | 213 | 33 | **366** |
| Plant species observed | 23 | 30 | 26 | 21 | **31** |
| Plant species visited | 3 | 12 | 12 | 8 | **20** |
| | | | | | |
| **Visitor types** | | | | | |
| bees | 1 | 9 | 6 | 2 | **12** |
| wasps | 0 | 1 | 4 | 1 | **4** |
| ants | 0 | 1 | 1 | 1 | **1** |
| flies | 2 | 1 | 3 | 0 | **5** |
| bugs | 0 | 0 | 1 | 0 | **1** |
| butterflies and moths | 0 | 1 | 1 | 0 | **1** |
| **Total** | **3** | **13** | **16** | **4** | **26** |
| | | | | | |
| **Interaction types** | | | | | |
| bees | 1 | 14 | 10 | 3 | **22** |
| wasps | 0 | 1 | 4 | 1 | **6** |
| ants | 0 | 3 | 5 | 6 | **9** |
| flies | 2 | 1 | 4 | 0 | **6** |
| bugs | 0 | 0 | 1 | 0 | **1** |
| butterflies and moths | 0 | 1 | 1 | 0 | **2** |
| **Total** | **3** | **20** | **25** | **10** | **46** |
| | | | | | |
| **Visits** | | | | | |
| bees | 194 | 2 | 75 | 107 | **10** |
| wasps | 47 | 0 | 13 | 28 | **6** |
| ants | 91 | 0 | 4 | 70 | **17** |
| flies | 27 | 6 | 16 | 5 | **0** |
| bugs | 2 | 0 | 0 | 2 | **0** |
| butterflies and moths | 5 | 0 | 4 | 1 | **0** |
| **Total** | **366** | **8** | **112** | **213** | **33** |
| **Interaction frequency** | | | | | |
| bees | 100 | 590 | 377 | 79 | **1146** |
| wasps | 0 | 28 | 395 | 7 | **430** |
| ants | 0 | 40 | 169 | 316 | **525** |
| flies | 23 | 7 | 16 | 0 | **46** |
| bugs | 0 | 0 | 5 | 0 | **5** |
| butterflies and moths | 0 | 57 | 2 | 0 | **59** |
| **Total** | **123** | **722** | **964** | **402** | **2211** |

(e) Junction, June

| | **TP 1** | **TP 2** | **TP 3** | **TP 4** | **Overall** |
|---|---|---|---|---|---|
| Total visits | 55 | 202 | 297 | 124 | **678** |
| Plant species observed | 29 | 33 | 34 | 25 | **35** |
| Plant species visited | 4 | 18 | 22 | 11 | **27** |
| | | | | | |
| **Visitor types** | | | | | |
| bees | 3 | 14 | 22 | 8 | **35** |
| wasps | 0 | 4 | 8 | 2 | **10** |
| ants | 1 | 1 | 1 | 1 | **1** |
| flies | 1 | 3 | 2 | 1 | **5** |
| beetles | 0 | 4 | 6 | 0 | **8** |
| butterflies and moths | 0 | 1 | 2 | 2 | **5** |
| **Total** | **5** | **27** | **40** | **14** | **63** |
| | | | | | |
| **Interaction types** | | | | | |
| bees | 3 | 18 | 34 | 9 | **59** |
| wasps | 0 | 4 | 8 | 2 | **13** |
| ants | 1 | 2 | 5 | 2 | **7** |
| flies | 1 | 3 | 2 | 1 | **7** |
| beetles | 0 | 4 | 6 | 0 | **9** |
| butterflies and moths | 0 | 1 | 2 | 2 | **5** |
| **Total** | **5** | **32** | **56** | **16** | **99** |
| | | | | | |
| **Visits** | | | | | |
| bees | 408 | 9 | 100 | 205 | **94** |
| wasps | 56 | 0 | 12 | 23 | **21** |
| ants | 173 | 44 | 73 | 50 | **6** |
| flies | 16 | 2 | 10 | 3 | **1** |
| beetles | 14 | 0 | 6 | 8 | **0** |
| butterflies and moths | 11 | 0 | 1 | 8 | **2** |
| **Total** | **678** | **55** | **202** | **297** | **124** |
| | | | | | |
| **Interaction frequency** | | | | | |
| bees | 128 | 2063 | 6869 | 4592 | **13652** |
| wasps | 0 | 506 | 819 | 672 | **1997** |
| ants | 337 | 810 | 577 | 70 | **1794** |
| flies | 15 | 260 | 426 | 3 | **704** |
| beetles | 0 | 51 | 222 | 0 | **273** |
| butterflies and moths | 0 | 13 | 73 | 670 | **756** |
| **Total** | **480** | **3703** | **8986** | **6007** | **19176** |

(f) Junction July

| | **TP 1** | **TP 2** | **TP 3** | **TP 4** | **Overall** |
|---|---|---|---|---|---|
| Total visits | 2 | 32 | 30 | 2 | **66** |
| Plant species observed | 8 | 12 | 12 | 9 | **12** |
| Plant species visited | 1 | 5 | 7 | 2 | **9** |
| | | | | | |
| **Visitor types** | | | | | |
| bees | 0 | 4 | 9 | 1 | **12** |
| wasps | 0 | 3 | 3 | 1 | **6** |
| flies | 1 | 2 | 0 | 0 | **2** |
| butterflies and moths | 0 | 2 | 1 | 0 | **3** |
| **Total** | **1** | **11** | **13** | **2** | **22** |
| | | | | | |
| **Interaction types** | | | | | |
| bees | 0 | 5 | 9 | 1 | **14** |
| wasps | 0 | 3 | 4 | 1 | **7** |
| flies | 1 | 2 | 0 | 0 | **2** |
| butterflies and moths | 0 | 2 | 1 | 0 | **3** |
| **Total** | **1** | **12** | **14** | **2** | **26** |
| | | | | | |
| **Visits** | | | | | |
| bees | 29 | 0 | 11 | 17 | **1** |
| wasps | 23 | 0 | 10 | 12 | **1** |
| flies | 7 | 2 | 5 | 0 | **0** |
| butterflies and moths | 7 | 0 | 6 | 1 | **0** |
| **Total** | **66** | **2** | **32** | **30** | **2** |
| | | | | | |
| **Interaction frequency** | | | | | |
| bees | 0 | 39 | 83 | 5 | **127** |
| wasps | 0 | 42 | 66 | 2 | **110** |
| flies | 16 | 23 | 0 | 0 | **39** |
| butterflies and moths | 0 | 28 | 5 | 0 | **33** |
| **Total** | **16** | **132** | **154** | **7** | **309** |

Appendix 11. Visitor species and morphospecies to multiple plant species and the time period in which they visit. The family for each visitor is given below the species name. Each acacia species is highlighted in a different colour.

| | **TP 1 (6.00-9.00)** | **TP 2 (9.00-12.00)** | **TP 3 (12.00-15.00)** | **TP 4 (15.00-18.00)** |
|---|---|---|---|---|
| **Turkana Boma, May** | | | | |
| *Tetralonia boharti*<br>bee; Apidae | | *Hibiscus flavifolius*<br>*Abutilon mauritianum* | | |
| *Apis mellifera*<br>bee; Apidae | | | *Ocimum forskolei*<br>*Senegalia brevispica* | *Ocimum forskolei*<br>*Croton dichogamus*<br>*Lippia kituiensis* |
| *Halictus* (*Seladonia*) sp. 1<br>bee; Halictidae | | ?*Becium* sp.<br>*Evolvulus alsinoides* | *Justicia lorata* | |
| *Lasioglossum* (*Dialictus*) sp. 1<br>bee; Halictidae | *Ipomoea sinensis* | *Ipomoea sinensis*<br>*Hibiscus flavifolius* | | |
| *Patellapis* (*Zonalictus*) sp. 1<br>bee; Halictidae | | *Felicia muricola*<br>*Ocimum forskolei* | | |
| *Pseudapis* (*Pseudapis*) sp. 1<br>bee; Halictidae | | *Indigofera volkensii* | *Melhania ovata*<br>*Senegalia brevispica* | |
| *Lipotriches* (*Lipotriches*) sp. B<br>bee; Halictidae | | | *Justicia lorata*<br>*Indigofera volkensii* | *Indigofera volkensii* |
| *Megachile* (*Chalicodoma*) sp. 2<br>bee; Megachilidae | | | *Gutenbergia cordifolia*<br>*Ocimum forskolei* | |
| Osmiini sp. e<br>bee; Megachilidae | | | Asteraceae spp. yellow<br>*Gutenbergia cordifolia* | *Gutenbergia cordifolia* |
| Bombyliidae sp. 1<br>fly; Bombyliidae | | *Helichrysum glumaceum*<br>*Evolvulus alsinoides* | | |
| Bombyliidae sp. 2<br>fly; Bombyliidae | | *Pentanisia ouranogyne* | *Melhania ovata* | |
| *Phytomia incisa*<br>fly; Syrphidae | *Lippia kituiensis* | *Senegalia brevispica*<br>*Croton dichogamus* | *Senegalia brevispica*<br>*Lippia kituiensis* | *Senegalia brevispica* |

| **Turkana Boma, May (cont.)** | **TP 1 (6.00-9.00)** | **TP 2 (9.00-12.00)** | **TP 3 (12.00-15.00)** | **TP 4 (15.00-18.00)** |
|---|---|---|---|---|
| *Eristalinus taeniops*<br>fly; Syrphidae | | Asteraceae spp. yellow<br>*Senegalia brevispica* | | |
| *Pretoriamyia* sp. 1<br>fly; Tachinidae | *Senegalia brevispica*<br>*Vachellia gerrardii* | *Senegalia brevispica*<br>*Vachellia gerrardii* | *Vachellia gerrardii* | |
| Mysotophilidae sp.<br>fly; Sarcophagidae | *Balanites* sp. | *Balanites* sp.<br>*Lippia kituiensis*<br>Asteraceae spp. yellow | *Balanites* sp.<br>*Lippia kituiensis* | *Balanites* sp.<br>*Felicia muricola* |
| *Megalognatha meruensis*<br>beetle; Chrysomelidae | | *Vachellia gerrardii* | | *Senegalia brevispica* |
| Alticinae sp. 1<br>beetle; Chrysomelidae | | *Lippia kituiensis*<br>*Helichrysum glumaceum* | | *Croton dichogamus* |
| *Lycus serenus*<br>beetle; Lycidae | | *Lippia kituiensis* | | *Felicia muricola* |
| *Coryna ?ambigua*<br>beetle; Meloidae | | *Gutenbergia cordifolia* | *Melhania ovata* | |
| Arctiidae sp.<br>moth; Arctiidae | | | | *Lippia kituiensis*<br>*Senegalia brevispica*<br>*Vachellia gerrardii* |
| **Turkana Boma, June** | | | | |
| *Apis mellifera*<br>b; Apidae | | *Monechma* sp. B<br>*Abutilon mauritianum* | *Monechma* sp. B | *Lippia kituiensis* |
| *Lasioglossum* (*Dialictus*) sp. 2<br>b; Halictidae | | *Plectranthus caninus* | *Hibiscus flavifolius* | |
| *Patellapis* sp. A<br>b; Halictidae | | *Ipomoea ficifolia*<br>*Hibiscus vitifolius* | | |
| *Lipotriches* (*Lipotriches*) sp. 1<br>b; Halictidae | | *Gutenbergia cordifolia*<br>*Abutilon mauritianum* | *Gutenbergia cordifolia*<br>*Senegalia brevispica* | |
| *Halictus* (*Seladonia*) sp. C<br>bee; Halictidae | | | *Gutenbergia cordifolia*<br>*Sida ovata*<br>*Abutilon mauritianum* | *Ipomoea obscura* |

| **Turkana Boma, June (cont.)** | **TP 1 (6.00-9.00)** | **TP 2 (9.00-12.00)** | **TP 3 (12.00-15.00)** | **TP 4 (15.00-18.00)** |
|---|---|---|---|---|
| *Heriades* (*Heriades*) sp. 1<br>bee; Megachilidae | | *Plectranthus caninus*<br>*Ocimum forskolei* | *Ocimum forskolei* | |
| *Megachile* (*Chalicodoma*) sp. 2<br>bee; Megachilidae | | *Monechma* sp. B | | *Gutenbergia cordifolia* |
| *Megachile* (*Pseudomegachile*) sp. 1<br>bee; Megachilidae | | *Justicia diclipteroides* | | *Gutenbergia cordifolia* |
| *Coryna ?apicornis*<br>beetle; Meloidae | | *Hibiscus aponeurus*<br>*Hibiscus flavifolius* | *Hibiscus aponeurus*<br>*Hibiscus vitifolius*<br>*Ipomoea ficifolia* | |
| **Turkana Boma July** | | | | |
| *Ceratina nyassensis*<br>bee; Halictidae | | | *Barleria spinisepala*<br>*Commelina* spp. blue<br>*Ipomoea sinensis* | |
| **Turkana Boma August** | | | | |
| *Xylocopa somalica*<br>bee; Apidae | | *Solanum* sp. 1<br>*Leucas glabrata* | *Vachellia etbaica*<br>*Leucas glabrata* | |
| *Apis mellifera*<br>bee; Apidae | | *Sida schimperiana*<br>*Commelina* spp. blue<br>*Leucas glabrata*<br>*Vachellia etbaica* | *Vachellia etbaica*<br>*Senegalia brevispica* | *Vachellia etbaica*<br>*Senegalia brevispica* |
| *Plebeina hildebranti*<br>bee; Apidae | | *Phyllanthus sepialis*<br>*Senegalia brevispica* | *Euphorbia* sp.<br>*Senegalia brevispica*<br>*Solanum* sp. 1 | |
| *Patellapis* sp. C<br>bee; Halictidae | *Polygala sphenoptera* | *Polygala sphenoptera* | *Gutenbergia cordifolia* | |

| **Junction June** | **TP 1 (6.00-9.00)** | **TP 2 (9.00-12.00)** | **TP 3 (12.00-15.00)** | **TP 4 (15.00-18.00)** |
|---|---|---|---|---|
| *Amegilla calens*<br>bee; Apidae | *Leucas glabrata* | *Solanum* sp. 1 | | |
| *Amegilla penicula*<br>bee; Apidae | | *Solanum* sp. 1 | | *Echiochilon lithospermoides* |
| *Apis mellifera*<br>bee; Apidae | | *Ipomoea kituiensis*<br>*Monechma* sp. B | *Hypoestes forskahlii*<br>*Emilia discifolia* | *Leucas glabrata*<br>*Monechma* sp. B |
| *Ceratina moerenhouti*<br>bee; Apidae | | | *Monechma* sp. B<br>*Heliotropium steudneri* | |
| *Pseudapis* (*Pseudapis*) sp. 1<br>bee; Halictidae | | | *Helichrysum glumaceum*<br>*Endostemon tereticaulis*<br>*Solanum* sp. 1 | |
| *Patellapis* sp. A<br>bee; Halictidae | *Ipomoea kituiensis* | | *Monechma* sp. B | |
| *Heriades* (*Heriades*) sp. 1<br>bee; Megachilidae | | *Plectranthus caninus*<br>*Monechma* sp. B | | *Ocimum forskolei* |
| Osmiini sp. e<br>bee; Megachilidae | | | *Monechma* sp. B<br>*Gutenbergia cordifolia*<br>*Justicia lorata* | |
| *Ammophila* sp. 1<br>wasp; Sphecidae | | *Leucas glabrata* | *Heliotropium steudneri* | |
| Alticinae sp. 1<br>beetle; Chrysomelidae | | *Sida ovata* | *Solanum* sp. 1 | |
| **Junction July** | | | | |
| Eumenidae sp. 9<br>wasp; Eumenidae | | *Hypoestes forskahlii* | | *Monechma* sp. B |

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