Pollination ecology of acacias (Fabaceae, Mimosoideae)

Graham N. Stone[A,E], *Nigel E. Raine*[B], *Matthew Prescott*[C] *and Pat G. Willmer*[D]

[A]Institute of Cell, Animal and Population Biology, University of Edinburgh, The King's Buildings,
West Mains Road, Edinburgh EH9 3JT, UK.
[B]Laboratory of Apiculture and Social Insects, Animal and Plant Sciences, University of Sheffield,
Sheffield, S10 2TN, UK.
[C]The Department of Zoology, Oxford University, South Parks Road, Oxford OX1 3PQ, UK.
[D]School of Biology, St Andrews University, Bute Building, St Andrews, KY16 9TS, UK.
[E]Corresponding author; email: graham.stone@ed.ac.uk

Abstract. We review the pollination ecology of acacias worldwide, discussing (1) the rewards provided to flower visitors, (2) the temporal patterns of flowering and reward provision and (3) the taxonomic composition of flower visitor assemblages. The flowers of most acacias (including all members of the subgenus *Phyllodineae*) offer only pollen to flower visitors and floral nectar is limited to a minority of species in the subgenera *Acacia* and *Aculeiferum*. The most important pollinators of acacias are social and solitary bees, although other insects and nectar-feeding birds are important in specific cases. Acacias that secrete nectar attract far more species-rich assemblages of flower visitors, although many of these are probably not important as pollinators. Most acacias in the subgenus *Phyllodineae* have long-lived protogynous flowers, without clear daily patterns in reward provision and visitation. In contrast, most members of the other two subgenera have flowers that last for a single day, appear to be protandrous and have clear daily patterning in reward provision and visitation. The generality of these patterns should not be assumed until the pollination ecology of many more phyllodinous acacias has been studied, particularly in arid environments. The accessibility of the floral rewards in acacia flowers makes them important examples of two general issues in plant communities—the partitioning of shared pollinators and the evolution of floral ant repellents.

Introduction

Acacias are dominant woody plants in many tropical and subtropical habitats, particularly in semi-arid regions across the world (Ross 1981). They are valuable as sources of timber, fruits and secondary plant compounds for many human societies (e.g. Turnbull 1987; Beentje 1994; Midgely and Turnbull 2003) and support an enormous biomass and diversity of invertebrate and vertebrate herbivores (Krüger and McGavin 1998). A number of acacias have also become serious pests following human introductions in Australia and southern Africa (Milton and Moll 1982; Morgan *et al.* 2002; Radford *et al.* 2002; Paynter *et al.* 2003). Although pollination and seed set are crucial aspects of acacia biology, they remain unstudied for most species. Understanding the link between floral visitation and seed set not only reveals links between plants and the biodiversity of flower visitors, but will also be crucial to understanding factors which may limit recruitment in endangered acacias and assessing the impact of invading species on native floras throughout the world. This is nowhere more true than in south-western Australia, where many species exist as local and fragmented populations in highly disturbed habitats.

This review has two aims. First, we briefly review what is known of the flower-visitor assemblages, floral rewards and flowering phenology of acacias across the world, and identify the taxa that are likely to represent important pollinators. Second, we discuss important general issues in community biology and symbiosis which have arisen from work on acacia pollination—specifically, the structuring of flowering phenologies in plant communities in response to the sharing of pollinators (Stone *et al.* 1996, 1998; Raine 2001) and the interactions between trees, ants and pollinators in those acacias that support ant guards (Willmer and Stone 1997; Raine *et al.* 2002).

Acacias have long been divided into the following three subgenera: *Acacia*, *Aculeiferum* and *Phyllodineae* (=*Heterophyllum*) (Maslin 2001). These taxa are now not regarded as forming a single monophyletic genus, but are thought to represent at least three radiations within a group of closely related mimosoid clades (Chappill and Maslin 1995; Robinson and Harris 2000; Maslin 2001; Miller and Bayer 2001). These groups share many basic mimosoid floral traits, which make it meaningful to consider them together, but they also differ in several important respects. First, while the subgenera *Acacia* and *Aculeiferum* are found in America, Africa, Eurasia and Australasia, the subgenus *Phyllodineae* has a more limited distribution centred on Australia (Ross 1981). These regions show characteristic differences in their insect faunas (particularly the relative rarity of social bees in Australia; Roubik 1989), which result in different pollinator assemblages. Second, the *Phyllodineae* differ markedly from the majority of species in the other two subgenera in several important aspects of their floral biology that are important for pollinators, as highlighted below.

Our review draws, in particular, on a large body of work on Australian acacias (mainly in the subgenus *Phyllodineae*) (Ford and Forde 1976; Bernhardt *et al.*1984; Bernhardt and Walker 1984; Knox *et al.* 1985; Bernhardt 1987; Vanstone and Paton 1988; Sedgley and Harbard 1993; M. Prescott, unpubl. data), detailed community studies in Senegal, Kenya and Tanzania in Africa (Tybirk 1989, 1993; Stone *et al.* 1996, 1998, 1999) and a detailed community study in western Mexico (Raine 2001). The literature on pollination in other habitats is surprisingly sparse and further details have been drawn from broader studies on the ecology of tropical trees (e.g. Zapata and Arroyo 1978), detailed analyses of the reproductive biology of single species (Peralta *et al.* 1992, Baranelli *et al.* 1995 for *A. caven*; Tandon *et al.* 2001, Diallo *et al.* 1997 for *A. senegal*; and Willmer and Stone 1997 for *A. zanzibarica*) and studies on the ecology of ant–acacia interactions (Janzen 1966, 1967; Hocking 1970; Raine *et al.* 2002).

Acacia floral rewards

The reproductive biology of acacia flowering is reviewed in detail by Kenrick (2003) and only relevant points will be summarised here. All have flowers presented in flower heads. These heads have often been termed 'inflorescences' in the past, although as defined by the Flora of Australia (vol. 11A, Mimosaceae, *Acacia* part 1), the term 'inflorescence' more properly applies to groups of flower heads on a floral shoot. Here, for clarity we will use the term flower head throughout. The structure of *Acacia* flower heads ranges from spherical (globose) to elongate (spicate) across species within each subgenus (Fig. 1). The number of flowers per flower head and the number of stamens per flower vary within species and more substantially among species; globose flower heads may contain as few as three flowers,

while spicate flower heads may contain more than 500 (Kenrick 2003). Each stamen bears an anther containing eight compound pollen grains, termed polyads (Kenrick 2003). In some acacia species, all flowers are hermaphrodite, with a single central stigma, while in others a proportion of flowers on an individual tree are purely male (Table 1, discussed below).

Floral rewards to pollinators are of two main types, pollen and nectar. In all acacias, the polyads are presented on the surface of the flower head (Kenrick 2003) and any nectar is accessible only to those insects with mouthparts long enough to enter the corolla tube of the flowers. In contrast to many other flower structures, acacia flowers have no complex morphological traits that allow access only to specific visitor taxa. As a consequence, a wide variety of insects and some birds visit acacia flowers (discussed below) and the resources offered by the flowers are vulnerable to raiding by non-pollinators. The morphology of acacia flowers may be responsible for the evolution of alternative defences, particularly the ant repellents discussed below.

(a) Pollen

Acacia species vary in the size and number of pollen grains incorporated into each polyad (4, 8, 16 or 32, with a most common value of 16; Kenrick and Knox 1982, 1989; Kenrick 2003). Pollinators harvest polyads as units and their size and nutritional value may be a factor in choice of forage plant (Bernhardt and Walker 1984). In some assemblages there is little variation in polyad size (Stone *et al.* 1998) and here and elsewhere the spatial presentation of pollen is probably more important for pollen-harvesting visitors. The number of stamens per flower and the number of flowers per flower head both vary substantially within and among species (Tybirk 1989, 1993; Sedgley *et al.* 1992; Kenrick 2003; Table 1, Fig. 1). The number of polyads offered by a flower head is the sum of the number of flowers multiplied by the number of stamens per flower, multiplied by a constant eight polyads per anther, and this sum thus also varies substantially across sympatric acacia species (Table 1). For example, *Acacia drepanolobium* offers *c.* 19 000 polyads per flower head, while *A. nilotica* offers *c.* 51 000. The density of flower heads on the plant also varies enormously: for example, while *A. drepanolobium* has a small number of flowers per head (Table 1, Fig. 1*a*), flowering trees are often covered in a dense mass of inflorescences. In contrast, *A. nilotica* has many flowers per head (Table 1, Fig. 1*b*), but a far lower density of flower heads on a tree at any given time than *A. drepanolobium*. These differences in the presentation of resources may well be significant for flower visitors, although no study has yet examined this issue in detail. Data from Tanzania show that larger bees [such as *Xylocopa* carpenter bees and honeybees (*Apis mellifera*)] only visit species with dense, flower-rich heads (such as *Acacia nilotica* and *A. tortilis*) and avoid species with
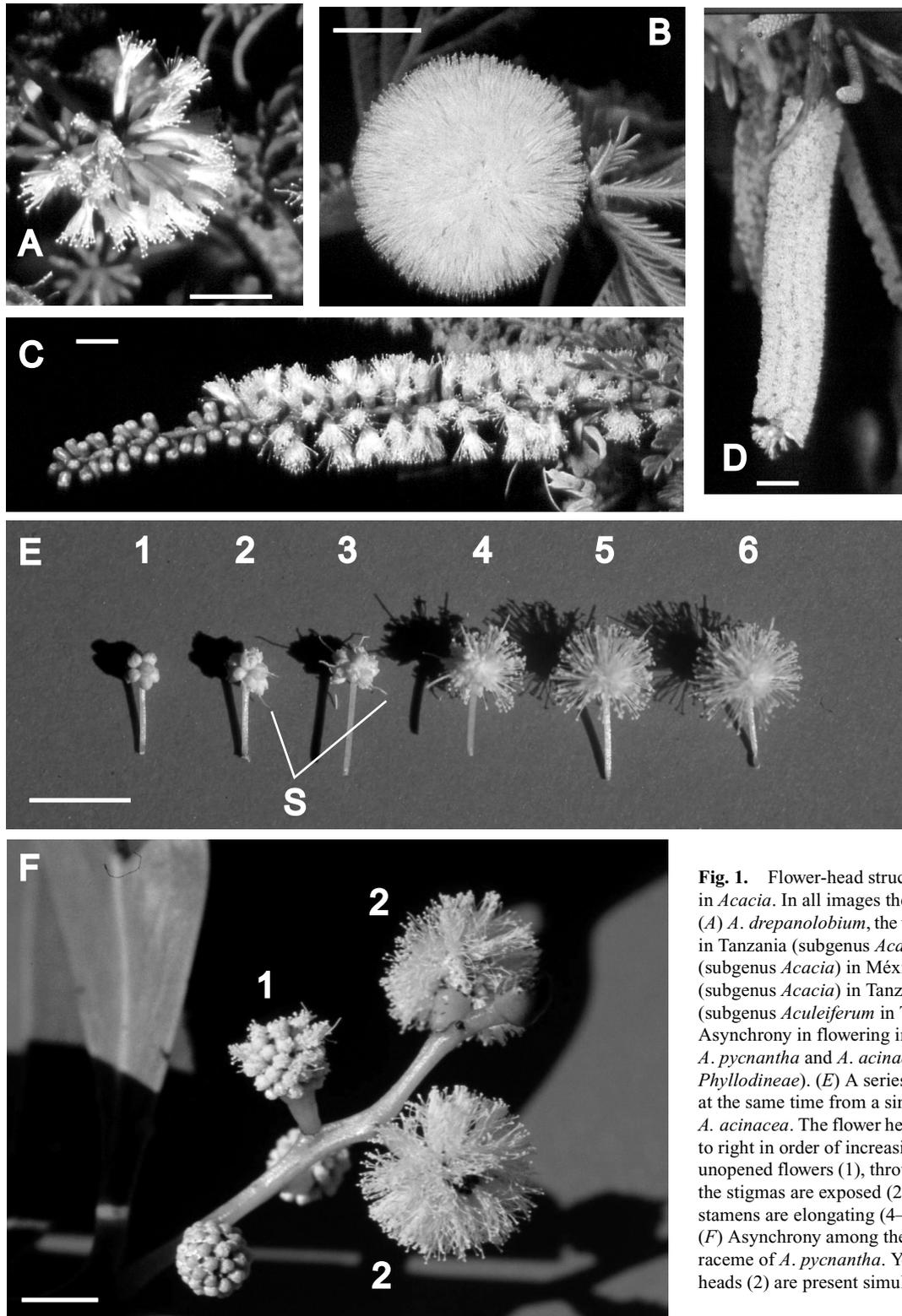
Fig. 1. Flower-head structure and floral phenology in *Acacia*. In all images the scale bar = 5 mm. (*A*) *A. drepanolobium*, the whistling thorn ant acacia, in Tanzania (subgenus *Acacia*). (*B*) *A. hindsii* (subgenus *Acacia*) in México. (*C*) *A. nilotica* (subgenus *Acacia*) in Tanzania. (*D*) *A. senegal* (subgenus *Aculeiferum* in Tanzania. (*E*, *F*) Asynchrony in flowering in the Australian acacias *A. pycnantha* and *A. acinacea* (subgenus *Phyllodineae*). (*E*) A series of flower heads sampled at the same time from a single individual of *A. acinacea*. The flower heads are arranged from left to right in order of increasing flower-head age, from unopened flowers (1), through flowers in which only the stigmas are exposed (2, 3) to those in which the stamens are elongating (4–6). S = style. (*F*) Asynchrony among the flower heads on a single raceme of *A. pycnantha*. Young heads (1) and older heads (2) are present simultaneously.

Table 1.   Variation in the mean number of flowers per flower head and stamens per flower in *Acacia* species in Tanzania (Stone *et al.* 1999) and in Mexico (Raine 2001)

Total number of polyads is calculated as (the number of flowers) × (the number of stamens) × (8 polyads per anther). Errors are ± 1 standard error. In Tanzania, values are means for 10 flowers from each of 10 flower heads for two individuals of each species. In Mexico, values are means for 10 flowers from each of 10 flower heads for between three and six individuals of each species

Acacia species	Flowers per head	Stamens per flower	Polyads per flower head	Flowers with a stigma (%)
		Tanzania		
A. drepanolobium	27.8 ± 2.1	56.4 ± 2.3	19040	70 ± 9.7
A. nilotica	92.2 ± 1.2	68.7 ± 1.5	50673	13 ± 9.0
A. senegal	83.7 ± 7.6	68.2 ± 1.4	45666	90 ± 3.3
A. zanzibarica	42.2 ± 4.5	56.4 ± 2.3	19040	62.0 ± 11.3
		Mexico		
A. angustissima	16.6 ± 0.7	262.3 ± 15.2	34480	84 ± 1.5
A. cochliacantha	48.5 ± 4.5	47 ± 2.8	18236	31 ± 1.9
A. farnesiana	60 ± 6.6	47.2 ± 1.5	22656	77 ± 1.1
A. hindsii	209 ± 6.8	90 ± 8.6	150480	100 ± 0.0
A. macracantha	73.7 ± 5.4	66.9 ± 8.2	39444	82 ± 1.9

very sparse flower heads (such as *A. drepanolobium*). Such behaviour is in part to be expected from the economics of harvesting pollen: large bees need to visit a larger number of sparse flower heads to gather a pollen load of given size and flying between flower heads is certainly more energetically costly than harvesting from a single flower head (Heinrich and Heinrich 1983; Bernhardt and Walker 1984). Observations of honeybees on a range of *Acacia* species also suggest that flower heads with a small number of flowers are unable to support the weight of a large bee on their surface and tend to collapse, making foraging more difficult. In contrast, very small bees are able to gather a full pollen load from even sparse flower heads and are represented in the flower-visitor assemblages of all acacias so far studied. Such issues may be important determinants of pollinator assemblages for sympatric acacias.

Many acacias produce flowers (and often entire heads of flowers) containing only stamens (Table 1; see also Tybirk 1989; Sedgley *et al.* 1992; Baranelli *et al.* 1995; Kenrick 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 of the tissues producing floral scents are located in the anthers and associated structures (Tybirk 1993; Kenrick 2003) and large numbers of purely staminate flowers represent a powerful visual and olfactory advertisement. Such advertisement may be particularly important if co-flowering acacias compete for pollination (Bernhardt and Walker 1984; see below).

(b) Floral nectar

Secretion of floral nectar is not common in acacias. Floral nectar is secreted by some species in the subgenera *Acacia* (e.g. *A. zanzibarica* and *A. tortilis* in Tanzania) and *Aculeiferum* (*A. brevispica*, *A. mellifera*, *A. senegal*) (Stone

et al. 1998; Tandon *et al.* 2001) but is unknown in *Phyllodineae* (Sedgley 1989; Kenrick 2003). The quality and quantity of nectar secreted also varies substantially among species. Flowers of *A. senegal* secrete abundant dilute nectar in the early morning, the concentration increasing and the volume decreasing as a result of nectar harvesting and evaporative water loss (Fig. 2). In contrast, *A. zanzibarica* secretes tiny volumes (≪1 μL) of highly concentrated nectar (*c.* 70% sucrose by mass) per flower. Visits by obligate nectar-feeding insects to other species suggest that these too may secrete nectar. *A. tortilis* is visited by a wide diversity of nectar-feeding insects (Table 2; Tybirk 1993; Stone *et al.* 1998, 1999), although dissections revealed no nectary (Tybirk 1993). Tybirk (1993) interpreted this as deception of pollinators by the plant. However, an alternative interpretation is that the flowers of *A. tortilis* do indeed secrete small volumes of a fluid harvested by foragers.

(c) Extrafloral nectar

Acacias also possess extrafloral nectaries on the petiole and rachis of the leaves. The role of these glands in attracting pollinators remains little studied, but the presentation of this nectar in open, cuplike glands makes it accessible to a wide range of foragers (Bernhardt 1987). Bees harvesting pollen from the nectarless flowers of Australian phyllodinous acacias have been observed harvesting nectar from extrafloral nectaries on the same plant (Bernhardt and Walker 1984) and extrafloral nectaries remote from the flowers can thus function as an effective reward for these foragers. However, extensive observations of the Australian acacias in Table 3 by one of us (M. P.) recorded only ants and wasps as visitors to extrafloral nectaries, and it is clear that bee exploitation of this resource is not widespread, either within or across phyllodinous acacia species. The need to compensate for nectarless flowers when attracting bees
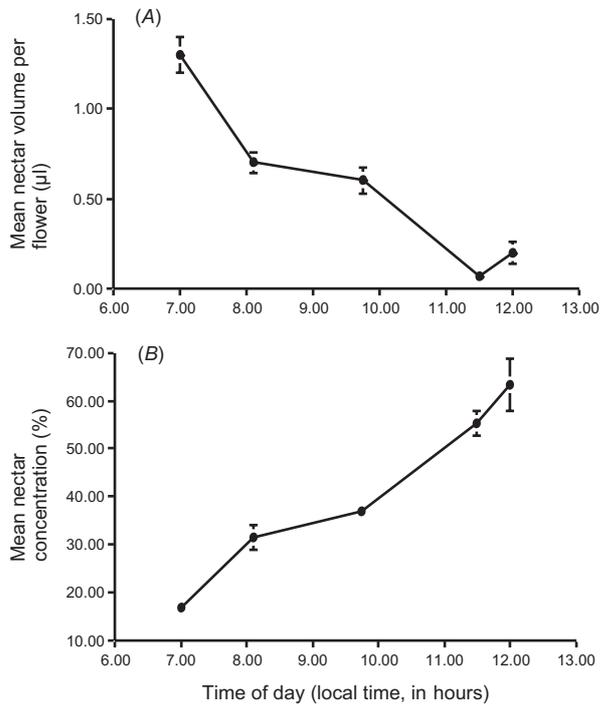
Fig. 2. Daily patterns of nectar secretion in *Acacia senegal* in Mkomazi Game reserve, Tanzania (Stone *et al.* 1998). Nectar was sampled from one individual on 21 December 1995, sampling 10 flower heads per datum. (*A*) Mean nectar volume per flower. (*B*) Mean nectar concentration (% sucrose by mass). Values are means ± 1 standard error.

(Bernhardt and Walker 1984) is nevertheless an interesting alternative hypothesis that merits further study.

In at least two Australian species, *A. pycnantha* (subgenus *Phyllodineae*; Ford and Forde 1976; Vanstone and Paton 1988) and *A. terminalis* (subgenus *Aculeiferum*; Knox *et al.* 1985), the petiole glands attract assemblages of nectar-feeding birds. In both species, the heads of birds (particularly silvereyes, thornbills and spinebills) probing for nectar come into contact with neighbouring flower heads and the head, neck and shoulders become coated with polyads. The significance of bird visitation in *A. pycnantha* is shown by the demonstration that exclusion of flower-visiting honeyeaters, silver eyes and thornbills significantly reduced pod production (Vanstone and Patton 1988). In *A. terminalis*, flowering branches bear paired racemes of flower heads interspersed by leaves bearing a single enlarged, bright red petiole gland. Extrafloral nectaries in other acacias are not so pigmented, suggesting the evolution of visual advertisement of the nectar reward. *A. terminalis* attracts groups of from three to a dozen birds in three passerine families (Acanthizidae, Meliphagidae and Zosteropidae), suggesting a generalist bird-pollination strategy (Knox *et al.* 1985).

The observation of bird visitation to extrafloral nectaries in *A. pycnantha* raises a general issue in pollination studies; are these visitors the primary pollen vectors, or are other visitors equally or more important? *A. pycnantha* flowers have a distinctive sickly sweet scent and attract large numbers of flies, hoverflies and native bees, usually in significantly larger numbers than sympatric co-flowering acacias (Bernhardt and Walker 1984; M. Prescott, unpubl. data). And, although *A. pycnantha* is visited by birds, a high proportion of visits observed by one of us (M. P.) were destructive, with eastern rosellas (*Platycercus eximius*) and Crimson rosellas (*P. elegans*) either feeding on flower visitors or removing flowers to feed on sap exudates. Extrafloral nectar in acacias is best known as a reward for ant guards in African and American ant acacias (Janzen 1966; Hocking 1970; Raine *et al.* 2002), and these glands also attract large numbers of bull ants (*Myermecia simillima*) and jumping jacks (*Myermecia pilosa*), two of the most aggressive ants in southern Australia, to *A. pycnantha*. The extrafloral glands of *A. pycnantha* become enlarged and begin to secrete nectar up to 2 weeks before flowering begins (M. Prescott, unpubl. data). It is possible that, instead of recruiting bird pollinators, these glands are intended primarily to recruit ant guards to protect the flowers *against* those birds or insects that are flower predators. This illustrates the general point, discussed further below, that ant guards and pollinators capable of harvesting the same reward may come into conflict (Willmer and Stone 1997; Raine *et al.* 2002). This discussion highlights the need for experimental demonstration of pollinator efficacy (as carried out for bird visitors to *A. pycnantha* by Vanstone and Patton 1988). It is also important to realise that plant rewards will reflect the *net balance* of selective forces imposed by pollinators and that the same set of available rewards may recruit different pollinators in different populations of the same species. Exactly this situation has been described for *A. terminalis* by Kenrick *et al.* (1987), discussed further below.

The quality and quantity of nectar secreted by extrafloral nectaries remain unknown for almost all acacias, but it is clear that the size and activity of these glands varies dramatically across species. American ant acacias, such as *A. cornigera* and *A. hindsii*, have highly active glands showing a daily pulse in secretion of dilute nectar (Raine 2001; Raine *et al.* 2002). In contrast, although some African ant acacias certainly do secrete extrafloral nectar (T. Young, pers. comm., for *A. drepanolobium*), the volumes secreted are very small and we have yet to observe pollinators of African acacias visiting extrafloral nectaries.

(d) Anther glands

Many acacia flowers possess anthers glands—globular structures attached to the anther by a stalk (Tandon *et al.* 2001; Kenrick 2003). Our work on the time course of pollen presentation in several African acacia species has shown that the anther glands become erect on their stalks as the anthers dehisce, apparently as part of the process of anther opening.

Table 2. The species richness of insects visiting the flowers of some African acacias in Tanzania (from Stone *et al.* 1999) and in Kenya and Senegal (from Tybirk 1993)

In Tanzania, the percentage values are the mean percentage of the total of all visits to flower heads made by the given taxon. Summed percentages do not equal 100 due to visitation by taxa not shown. Total visits equal the number of observations contributing to the observed percentages. P, pollen reward only; N, abundant nectar; n = trace amounts of highly concentrated nectar

Acacia species	Bees	Bees (%)	Other Hymenoptera	Lepidoptera	Lepidoptera (%)	Beetles	Flies	Flies (%)	Total taxa	Total visits	Floral reward
Tanzania											
A. drepanolobium	2	99.3		1	0.2		2	0.3	5	930	P
A. nilotica	4	78		4	0		6	22	14	314	P
A. senegal	8	73.2		17	14.5		13	4.4	38	557	P+N
A. tortilis	4	53.5		4	0.5		22	46	30	468	P+n
A. zanzibarica	13	35		16	6.7		32	40.7	61	186	P+n
Kenya and Senegal											
A. albida	33		56	29		4	11		133		P+N
A. nilotica	32		17	0		9	0		58		P
A. senegal	24		45	48		24	8		149		P+N
A. tortilis	19		46	29		36	11		141		P+n

Table 3.   Flower phenology and longevity of some Australian *Acacia* species in the subgenus *Phyllodineae*, all of which are protogynous

For each species, data are given for flower-head longevity (the total period in days from the opening of the first flowers on a flower head to senescence of the flower head), the probable duration of female phase (based on stigma extension and visible state in open flowers, rather than on tested receptivity) and the probable duration of male phase (based on sampled pollen from anthers and the physical state of the stamens on open flowers. WA, Western Australia. Values are based on tracking cohorts of individually marked flower heads through their entire development

Acacia species	Location	Flower-head longevity (days)	Duration of female phase (days)	Duration of male phase (days)
A. aprica	WA wheatbelt	8–11	3–6	4–8
A. cochlocarpa	WA wheatbelt	5–12	2–10	2–5
A. genistifolia	Southern Vic.	6–12	3–6	4–6
A. pycnantha	Southern Vic.	6–10	4–5	2–5
A. paradoxa	Southern Vic.	5–8	2–4	2–4
A. dealbata	Southern Vic.	8–15	1–8	1–8
A. melanoxylon	Southern Vic.	5–9	3–5	3–4
A. acinacea	Southern Vic.	5–9	3–5	2–4
A. mearnsii	Southern Vic.	4–8	2–4	2–4

It is possible that these glands play a role in the production of floral scents, either to attract pollinators, or to repel ants (see below) or both. A proportion of the anther glands are lost over the lifespan of the flower head (in the species studied, one day) and it has been suggested that these glands may represent a food reward harvested by pollinators (Bernhardt 1983). Microscopic analyses of pollen loads collected in Tanzania shows that the pollen dusting the underside of syrphid hoverflies contains substantial proportions of anther glands (mean 15.8% of total load, $n = 20$ loads) and also of entire anthers (mean 13.5% of total load), although this does not confirm that these insects actually feed on these flower parts. Bee pollen loads generally contain very few anther glands (mean 0.2% of total load for each of honeybees on *A. senegal*, $n = 6$ loads, and for *Megachile* species across the acacia species, $n = 16$ loads), suggesting that bee foraging behaviours do not harvest these bodies (or harvest them by default and then reject them when packaging pollen into corbicula). Similar purity of bee pollen loads was noted by Tybirk (1989) in Kenya. The value of these glands as a reward requires further study. An alternative role of anther glands is as 'pseudopollen'—a mimetic device to attract pollinators to receptive stigmas before and after real pollen rewards are available. Separation of male and female functions in time (dichogamy) to reduce the risk of self-pollination is widespread in acacias and since pollen is often the only reward for pollinators, visitors are unlikely to visit clearly female-phase flowers. The anther glands are raised slightly above the flower head as a particulate layer, apparently resembling a powdery coating of pollen. If effective, they would promote visitation by pollen-seeking (and so pollen-carrying) insects in both protandrous and protogynous systems.

Finally, a number of large mammals and birds feed directly on the flowers. If a proportion of the flowers are not eaten but pollinated, then the superabundance of flowers in some acacias may represent a reward in itself. Dutoit (1990) has proposed that giraffes may be important pollinators of *A. nigrescens* in southern Africa. This is an intriguing story, although the extent to which other flower visitors contribute to seed set in this case has yet to be examined.

The timing of reward presentation

The longevity of acacia flowers varies dramatically between the subgenera *Acacia* and *Aculeiferum* on one hand and *Phyllodineae* on the other. These two groups are dealt with in turn.

(*a*) *The subgenera* Acacia *and* Aculeiferum

In most species in these two genera that have been studied, flowers open and senesce on a single day (Tybirk 1989, 1993; Stone *et al.* 1996, 1998; Tandon *et al.* 2001). In species with globose flower heads, flower opening is usually synchronous over the whole head in African species (*A. drepanolobium*, *A. etbaica*, *A. brevispica*, *A. seyal*, *A. zanzibarica*, *A. tortilis*, *A. reficiens*—Tybirk 1989, 1993; Stone *et al.* 1998) and in Mexican species (*A. angustissima*, *A. cochliacantha*, *A. macracantha*—Raine 2001). In species with spicate inflorescences, opening may occur on the same day over the whole flower head (e.g. *A. hindsii*—Raine 2001; Raine *et al.* 2002), or may be staggered such that groups of neighbouring flowers open on the same day, with those basal in the flower head opening first (*A. bussei*, *A. senegal*, *A. thomasii*—Tybirk 1993; Stone *et al.* 1998, 1999). In the absence of rain (which delays flower opening), the whole head flowers in 3 days or less (Tybirk 1993; Stone *et al.* 1998, 1999). In most African and Mexican species, individuals in the same habitat release their pollen synchronously, over a specific period of *c.* 2 h each day (Fig. 3*a*, Tybirk 1993; Stone *et al.* 1998; Raine 2001). The timing of pollen release is sensitive to microclimate, occurring later on more humid days (Fig. 3*b*), suggesting that drying of a dehiscent structure may be involved in pollen release in the anther. Notwithstanding microclimatic effects, timing of pollen release is also consistent between flowering seasons (in species that flower more than once each year) and between
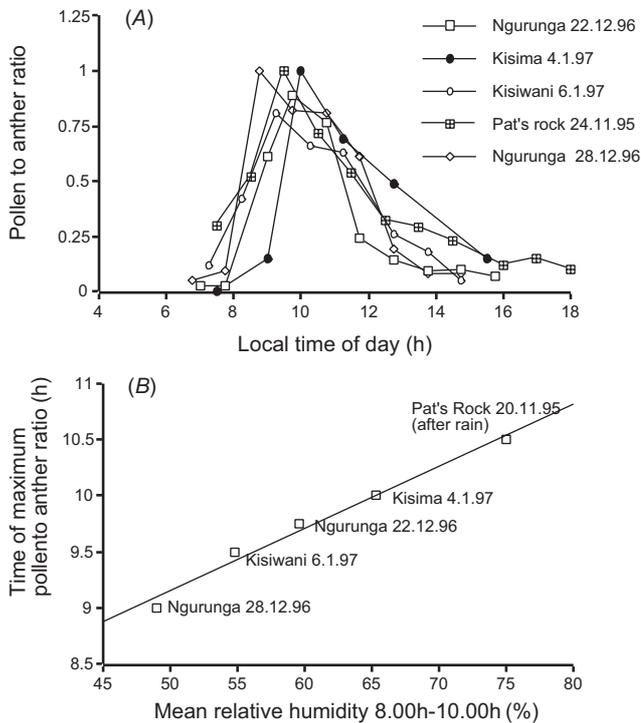
Fig. 3. (*A*) Intraspecific variation in patterns of pollen release over time between sites for *Acacia zanzibarica* in Mkomazi Game Reserve, Tanzania. Data points are means over individual trees at each site. (*B*) Timing of maximum pollen availability as a function of mean relative humidity over the period 0800–1000 hours for *A. zanzibarica*. The fitted line is a least squares regression, with equation $y = 0.055x + 6.381$, $r^2 = 0.983$, $P < 0.001$. Pollen release (dehiscence) in each species was evaluated by tracking changes in polyad abundance by methods described in full in Stone *et al.* (1998). To allow easy comparison between datasets, values for each are scaled to vary between 0 and 1 by dividing by the maximum value.

Fig. 4. Pollen release and bee activity for single trees of (*A*) *Acacia hindsii* in México (Raine *et al.* 2002) and (*B*) *A. tortilis* in Mkomazi Game Reserve, Tanzania (Stone *et al.* 1998). To allow the shapes of the distributions to be compared, values in each dataset are scaled to vary between 0 and 1 by dividing by the maximum value in the dataset. Pollen release is scored as described for Fig. 3. Pollinator activity was scored as visits per flower head, watching a consistent set of 20 flower heads.

years (Fig. 3a). In most species in the subgenera *Acacia* and *Aculeiferum*, flower opening involves extension of the stamens and release of the pollen, followed by later elongation of the stigmas. Initially at least, the stigmas are buried within a mass of stamens (e.g. Fig. 1*a–d*), suggesting that these species may be effectively protandrous (Tybirk 1989; Stone *et al.* 1998). However, Tandon *et al.* (2001) have shown for *A. senegal* that as long as pollen can reach the stigma, pollination is possible from 2 h before to 8–12 h after anther dehiscence. Further work on the timing of pollination in these species is required. In each species, pollen release is accompanied by a discrete burst of scent, usually strong and distinctive. Species offering nectar tend to produce sweet scents, while some species that are visited extensively by flies (such as *A. etbaica*) have a more musky scent.

There are exceptions to this rule. *A. farnesiana* is a widespread species in the subgenus *Acacia* and shows clear protogyny. Flower opening and fertilisation in this species is also far more protracted, extending over 4 days and there is little ev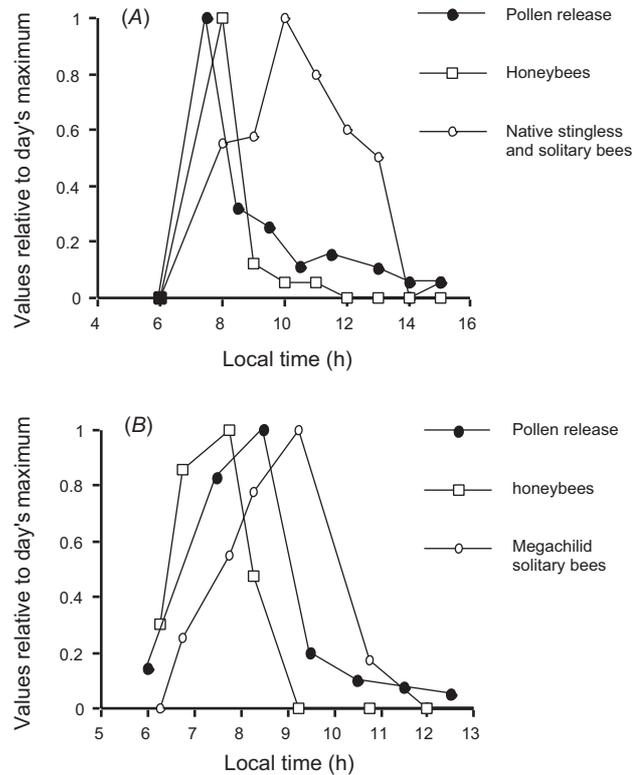idence of synchrony of flower heads within an individual (Raine 2001). *A. karroo*, from southern Africa, is protandrous, but retains stigmatic receptivity for up to 5 days after anther dehiscence (Sedgley and Harbard 1993). These examples of floral longevity parallel far more closely the pattern common in *Phyllodineae*.

(*b*) *The subgenus* Phyllodineae

In the subgenus *Phllodineae*, the majority of species examined are clearly protogynous (Sedgley and Harbard 1993; Kenrick 2003). Individual flowers usually remain in good condition for many days (although the anthers shrink and lose pigment a day or so after reaching full extension), and flowering is often asynchronous over a single tree and over a single flower head (Kenrick 2003; M. Prescott, unpubl. data) (Fig. 1*e*, *f*). The phenologies and durations of female and male phases of Australian acacias are shown in Table 3. The lack of synchrony within a flower head, and across trees within a population, may be important for flower visitors, since they make rapid harvesting of large pollen volumes from a single plant species more costly for large

bees. Instead, asynchrony on these two levels favours local foraging by smaller bees, for which a single flower, rather than a single flower head, is a significant resource. These differences may have major implications for the structuring of pollinator assemblages and for the way in which co-flowering acacias in the different *Acacia* subgenera interact (discussed below).

There are exceptions to this general pattern. Hybrids between *A. mangium* and *A. auriculiformis* produce flowers that are only weakly protogynous and last for only a single day (Sedgley *et al.* 1992; Sornsathapornkul and Owens 1998). It is probable that detailed studies on further species will reveal many more exceptions to the 'rules' outlined here. A major contrast between the taxa studied in Australia and those studied in Africa and America is that the former consist predominantly of species of relatively temperate habitats in southern Australia (Sedgley *et al.* 1992; M. Prescott, unpubl. data), while the latter grow in more highly seasonal, semi-arid environments. It is possible that the contrast in daily phenology between the *Phyllodineae* and the other subgenera is in part an artefact of this difference and more data are needed on the daily flowering behaviour of phyllodinous species in more arid habitats.

Acacia flower visitors

The open, accessible structure of acacia flower heads makes them accessible to a wide diversity of visitors, and in general visitor assemblages associated with mimosoid flowers are more diverse than those associated with more structurally complex legume flowers, such as the papilionoids (Arroyo 1981). The structure of visitor assemblages associated with acacia flowers is determined to a large extent by the local pool of potential visitors and the floral resources on offer. Acacias offering nectar and pollen are generally visited by more diverse insect assemblages than those offering only nectar, and even minute quantities of nectar suffice to recruit many obligate nectar-feeding species (Table 2; Tybirk 1993; Stone *et al.* 1998).

There is also evidence that interpopulation variation in floral dimensions may be correlated with differences in the pollinators recruited. For example, in *Acacia terminalis*, long-styled populations at lower altitudes are visited by birds, while short-styled populations at higher altitudes are visited by bees (Kenrick *et al.* 1987). In this case, longer styles may be necessary in the bird-pollinated population to achieve effective pollen transfer from birds visiting the extrafloral nectaries. Interpopulation variation in style length has also been reported for *A. senegal*, although its significance for pollinators has yet to be investigated (Tandon *et al.* 2001). Style length in many acacias in the subgenera *Acacia* and *Aculeiferum* changes extremely rapidly through the day and care must thus be taken when comparing lengths between populations.

Acacia flower visitors can be divided into the following three trophic groups: specialist pollen and flower feeders (bees, beetles, many of the true flies), specialist nectar feeders [birds, butterflies and bee flies (Bombyliidae)] and opportunist foragers (flies, ants and wasps). These visitors fulfil a range of roles and only a subset of them are effective pollinators. All acacias in the subgenera *Acacia* and *Aculeiferum* that have been studied release their pollen during the day and are pollinated by diurnal visitors. Nocturnal visitors (particularly beetles) certainly feed on the flowers, but are unlikely to be useful pollinators. It is possible that the more gradual pollen release seen in Australian phyllodinous acacias may yet be found to be associated with effective nocturnal pollinators.

(a) Birds

In addition to the birds recorded visiting extrafloral nectaries of Australian acacias (discussed above), several birds are recorded visiting acacia flowers. In Tanzania, sunbirds (*Nectarinia hunteri* and *N. venusta*, Nectariniidae) are known to visit *A. senegal* (Stone *et al.* 1988), and have also been recorded visiting flowers of *A. tortilis* in Mali [*Nectarinia pulchella* (Hagerup 1932)] and *A. nilotica* subsp. *indica* in India [*Nectarinia asiatica* and *N. zeylonica* (Arroyo 1981)]. While *A. senegal* secretes substantial volumes of nectar, *A. tortilis* (at least in Tanzania) secretes very little and *A. nilotica* none at all (Stone *et al.* 1998). It is possible that the sunbirds observed on *A. tortilis* and *A. nilotica* were either collecting pollen (van Tets and Nicolson 2000) or invertebrates (Hagerup 1932) to supplement the low levels of nitrogen in their diet (Roxburgh and Pinshow 2000). Whatever the reason for acacia visitation, these bird visitors have the potential to be highly effective long-distance pollen vectors.

(b) Bats

Very little is known about nocturnal visitation to acacia flowers in general. The only record we know of bat visitation to acacias is based on the analysis of pollen loads in the stomach contents of Mexican bats in the subfamily Glossophaginae (Alvarez and Gonzalez Quintero 1969). The *Acacia* species visited and the trophic reward collected by the bats in this case are unknown, although the Glossophaginae are predominantly nectar feeders (Alvarez and Sanchez-Casas 1999).

(c) Bees (Hymenoptera: Apoidea)

All acacias are visited by bees. Honeybees (several species in the genus *Apis*) are important pollinators both where they are native (Africa, South-east Asia) and where they are introduced (the Americas and Australia). In Tanzania, honeybees (*Apis mellifera*) are specific both in the *Acacia* species they visit, and the resources they collect from each species. In Tanzania, honeybees visited *A. senegal* only for its nectar, collected only pollen from *A. tortilis* and did not

visit *A. nilotica* flowering in the same vicinity at all (Stone *et al.* 1998). Two other studies, in Kenya and Senegal, recorded no honeybee visitation, in Kenya despite local farming of bees (Tybirk 1989). In Thailand, honeybees were frequent and effective pollinators to hybrids between *A. mangium* and *A. auriculiformis* (Sornsathapornkul and Owens 1998) and two other honeybee species (*Apis cerana* and particularly *Apis dorsata*) are important pollinators for *Acacia senegal* in northern India (Tandon *et al.* 2001). Introduced *Apis mellifera* are important flower visitors for acacias in Mexico (Raine 2001; Raine *et al.* 2002) and of some species (particularly those showing mass flowering) in Australia (Bernhardt and Walker 1984, 1985; Bernhardt *et al.* 1984; Bernhardt 1987; Sedgley *et al.* 1992). South America has a considerable diversity of other social bee groups and several stingless genera (*Trigona*, *Scaptotrigona*: Apidae) are important flower visitors for Mexican acacias (Raine 2001; Raine *et al.* 2002).

Solitary bees are important visitors to acacia wherever their pollination has been studied in depth. The same four families—Megachilidae, Colletidae, Halictidae and Anthophoridae—are important worldwide, with regional variation in the significance of particular families. In Tanzania and Kenya, important solitary bee genera include *Xylocopa* and *Amegilla* (Anthophoridae), *Nomia* (Halictidae) and *Megachile*, *Chalicodoma* and *Creightonella* (Megachilidae) (Tybirk 1989, 1993; Stone *et al.* 1998, 1999). In Mexico, the important solitary genera are *Ceratina*, *Exomalopsis* (Anthophoridae), *Halictus* (Halictidae), *Hylaeus* (Colletidae) and *Megachile* (Megachilidae) (Raine 2001; Raine *et al.* 2002), and Arroyo (1981) cites the significance of American desert acacias for the bee genus *Eulonchopria* (Colletidae). Except in the far-northern tropical forest, social bees are rarer in Australia than in the rest of the acacia distribution and solitary bee species are the dominant natural pollinators (Armstrong 1979; Bernhardt *et al.* 1984; Bernhardt 1987; Sedgley *et al.* 1992). The most important genera visiting four southern Australian acacias (*A. mitchelli*, *A. myrtifolia*, *A. pycnantha*, *A. retinodes*) are *Lasioglossum* (Halictidae) and *Leioproctus* (Colletidae) (Bernhardt and Walker 1984; Bernhardt *et al.* 1984; Bernhardt 1987). It is also noticeable that the native bees visiting southern Australian phyllodinous acacias are all small species (Bernhardt 1987; M. Prescott, unpubl. data), perhaps in keeping with the provision of small pollen rewards in non-synchronously flowering heads. It is worth noting that the significance of bee visitation appears highly variable among acacia species and between years. Surveys by Bernhardt found solitary bee visitation to be extremely significant (Bernhardt and Walker 1984; Bernhardt *et al.* 1984; Bernhardt 1987), while recent surveys by one of us (M. P.) found solitary bees to make up less than 10% of the visiting taxa and 1–5% of the flower visits to the *Acacia* species shown in Table 3.

Bees are the only flower visitors to actively collect large volumes of externally stored pollen, in contrast to almost all other flower visitors in which pollen collection is accidental. The dependence of bees on pollen for their brood means that they forage far beyond individual trophic requirements. In Tanzania, many of the same solitary bee species visited both nectar-secreting and nectarless *Acacia* species, and typically contributed a high proportion of all flower visits (Table 2). The direct link between pollen-harvesting efficiency and reproductive success in bees also promotes rapid handling times and high levels of movement between inflorescences and between trees (Tybirk 1993). The low levels of self-compatibility in most acacias (Hocking 1970; Janzen 1974; Zapata and Arroyo 1978; Bernhardt *et al.* 1984; reviewed by Kenrick 2003) suggest that this movement is crucial to outcrossing and seed set.

The foraging behaviour of some megachilid solitary bees, particularly *Megachile* species, suggests that they may be specialist pollinators of mimosoids with densely packed flower heads, including acacias. These bees somersault around the inflorescence, skimming rapidly over the exposed anthers, and are thus able to harvest acacia polyads far more rapidly than generalist foragers such as honeybees (Tybirk 1989; G. Stone, unpubl. data). Bernhardt (1989) reported vibratory pollen collection (buzz-pollination) by honeybees and *Lasioglossum* (Halictidae) visiting Australian acacias and we have seen similar behaviour in honeybees visiting *A. tortilis* in Tanzania. This harvesting mechanism has yet to be reported elsewhere.

(d) Flies (Diptera)

Acacia flowers are visited by a wide diversity of true flies (Diptera), most of which are pollen feeders (Gilbert 1981; Sedgley *et al.* 1992; Tybirk 1993; Stone *et al.* 1999). In Tanzania, this group includes six genera of hoverflies (family Syrphidae) and eight genera of pollen-feeding Rhiniinae (family Calliphoridae). The Rhiniinae, particularly the 11 species in the genus *Rhyncomya*, show very little movement even within trees (G. Stone, unpubl. data), and are probably insignificant pollen vectors. The larger hoverflies, in contrast, are particularly active insects and carry substantial pollen loads (see above and Sedgley *et al.* 1992). Despite the lower purity of their pollen loads (see above), these insects may be important pollen vectors.

(e) Butterflies (Lepidoptera)

Butterflies are obligate nectar feeders and are abundant only on acacias that secrete nectar (compare *A. senegal* and *A. nilotica* in Table 2) (Tybirk 1989; Stone *et al.* 1996; Tandon *et al.* 2001). Even when they are abundant, however, butterflies contribute only a low proportion of total flower visitation (compare bees and butterflies for *A. senegal* in Table 2), and their high stance on flowers tends to limit the accumulation of large pollen loads (Bernhardt 1989; Tybirk

1993; Tandon *et al.* 2001). While some of the larger butterflies that visit acacia, including species in the families Papilionidae, Nymphalidae and Pieridae, may be effective pollinators, many of the smaller species are extremely local in their movements. Acacias are important food plants for the larvae of many lycaenids (blues and their relatives) (Larsen 1991) and adults of 10 species were common on flowers of nectar-secreting acacias in Tanzania (Stone *et al.* 1999). Little of the time on the flowers was spent feeding; instead, the flower heads are important sites of sexual interaction.

(f) Beetles (Coleoptera)

Several studies have recorded beetles as flower visitors to acacias (Tybirk 1989; Willmer and Stone 1997; Raine 2001; Tandon *et al.* 2001). Although many diurnally active beetles are powerful fliers, most of those observed on African acacias are predators of flowers, particularly flower chafers (Scarabeidae, Cetoniinae) and blister beetles (Melioidae). These remain on individual flowers for much longer periods than other flower visitors, tend to occupy a single tree unless disturbed (Tybirk *et al.* 1993; Tandon *et al.* 2001; G. N. Stone, unpubl. data) and are unlikely to play a major role in pollination.

(g) Wasps and ants

Finally, a diversity of opportunist predators, particularly wasps and ants, visit acacia flowers either for nectar or for prey items. In Kenya and Tanzania, *Camponotus* ants collect the honeydew secreted by lycaenid butterfly caterpillars which feed on acacia flowers (van Noort and Stone 1999). In contrast to such tending behaviour, the flowers of acacias with symbiotic ant guards are very rarely visited by the resident ants—an issue discussed in detail below. A wide diversity of genera of solitary [e.g. *Scolia* (Scoliidae), *Bembix* (Bembicidae)] and social wasps [e.g. *Polistes* (Vespidae), *Delta* (Eumenidae)] have been observed foraging from acacia flowers (Tybirk 1993). Where these visits are to acacias that do not secrete nectar, a high proportion are probably in search of insect prey, such as the caterpillars of lycaenid butterflies (van Noort and Stone 1999) and geometrid moths (M. Prescott, unpubl. data) that feed on the flowers. The opportunistic nature of nectar collection from species such as *A. senegal* is supported by the observation that the extrafloral nectaries of Australian phyllodinous acacias are visited by similar assemblages of wasps (Bernhardt 1987).

Temporal patterns of insect activity at acacia flowers

For those acacias with a discrete daily peak, pollen release is followed rapidly by the arrival of pollen-harvesting bees and pollen-feeding flies (Tybirk 1989, 1993; Stone *et al.* 1998; Raine *et al.* 2002). Examples for *A. hindsii* in México and *A. tortilis* in Tanzania are shown in Fig. 4. Activity of other insects on flowers (e.g. flower-feeding beetles) tends not to

track pollen release and to extend over much of the day. As described above, release of pollen is accompanied by release of strong and distinctive scents and these probably function to recruit pollinators. If pollen release is indeed triggered by drying of tissues in the anthers, and the anthers also secrete a major proportion of the floral scent (Kenrick 2003), then reward and advertisement will occur synchronously despite variation in diurnal rhythms in relative humidity and temperature. Activity patterns of visitors to phyllodinous acacias in southern Australia are much more variable, and in the absence of any daily pattern in pollen release instead respond to fluctuation in microclimate (M. Prescott, unpubl. data).

Competition for pollination

In much of their range, and particularly in semi-arid habitats, acacias grow in species-rich assemblages. In Tanzania and Kenya, both centres of species richness for African acacias (Ross 1981), it is possible to find between 5 and 10 species in a square kilometre [Stone *et al.* 1998; Coe *et al.* 1999 for the Mkomazi Game Reserve, Tanzania; G. N. Stone and P. G. Willmer (unpubl. data) for the Mpala Research Centre, Laikipia, Kenya]. Richness in central and southern America tends on average to be lower than in Africa, while in Australia it can be substantially greater (Ross 1981; Maslin and Pedley 1982; Friedel *et al.* 1994; Maslin 2001). Even though there is substantial variation between locations and from year to year, it is common for a significant proportion of the acacia community in any one location to flower together (co-flower) during or immediately following seasonal rainfall (Bernhardt and Walker 1984; Milton 1987; Hopkins and Graham 1989; Sedgley *et al.* 1992; Tybirk 1993; Stone *et al.* 1998; Coe *et al.* 1999). The lack of a highly specific relationship between acacias and specific pollinators means that co-flowering acacias commonly share many of the same pollinators (Arroyo 1981; Bernhardt and Walker 1984; Sedgley *et al.* 1992; Stone *et al.* 1998; Raine 2001). This creates the potential for competition for pollination among individuals within species, and among acacia species. Competition for pollination in fact consists of two types of interaction (Rathcke 1983, 1988).

First, competition for the visits of shared pollinators—In cases where the quantity of pollen exchanged is a limiting factor for seed set, plants may compete for pollinator visits. Species or individuals with highly attractive rewards may monopolise the local visitor population to the detriment of other plants (Mosquin 1971; Horvitz and Schemske 1988).

Second, competition for pollen purity—If shared pollinators visit a mixture of flowering species over a short period, they carry a diversity of pollen types on their bodies and may deposit pollen from one species on the stigma of another. For some *Acacia* species pairs, this can result in viable hybrids (Leach and Whiffin 1978; Ali and Quaiser 1980; Sedgley *et al.* 1992). However, if viable hybrids are not

formed, occupation of the stigmatic cup by an inappropriate polyad (only one polyad can be accommodated in acacias; Kenrick and Knox 1982; Tandon *et al.* 2001; Kenrick 2003) will prevent fruit set in a given flower. This is seen as an important potential problem for plants that share pollinators (Waser 1978*a*, 1978*b*, 1983; Waser and Fugate 1986; Fishbein and Venable 1996).

In other plant communities, these potential problems are avoided either by evolutionary divergence in flowering seasons among potentially competing plant species, or by the exploitation of different pollinators (Pleasants 1980; Arroyo 1981; Rathcke 1988). However, neither option is available to co-flowering acacias. Bernhardt and Walker (1984) illustrated the reality of this issue for acacias with data for *A. pycnantha* and *A. myrtifolia* in Victoria, Australia. They found that *A. pycnantha* was far more attractive to insects than *A. myrtifolia* and that while pollen loads of bees caught on *A. pycnantha* were relatively pure (75% only contained *A. pycnantha* pollen), 54% of bees collected on *A. myrtifolia* carried the pollen of *A. pycnantha*. Although this appears to represent a serious problem for *A. myrtifolia*, the risk of stigmatic blockage is also affected by the relative size of the polyads of the species involved. The polyad of *A. pycnantha* is twice the size of the *A. myrtifolia* polyad and is probably too large to occupy and block the stigma of *A. myrtifolia*.

Data from an acacia community in Mkomazi Game Reserve, Tanzania, suggest that co-flowering species there have reduced the risk of interspecific pollen transfer by partitioning the activity of shared pollinators on a daily timescale (Stone *et al.* 1996, 1998). Pollen release is synchronous within each acacia species and each acacia species occupies a different time window (Table 4, Fig. 5). As illustrated above, pollinators rapidly recruit to each *Acacia* species, exhausting available pollen before moving on to the next *Acacia* species in the daily sequence. The peak pollen availabilities of the co-flowering *Acacia* species are evenly spaced between dawn and dusk, as predicted by resource-partitioning theory (Poole and Rathcke 1979; Williams 1995; Stone *et al.* 1996).

The logic of this argument leads to several testable predictions. If competition for pollination is responsible for the synchrony we see within species, then species (or populations) that flower alone (either in space or time) and so have no potential competitors, should show less synchrony in daily pollen release. This prediction is supported both across species in Tanzania (Stone *et al.* 1998) and within species in Mexico (Raine 2001).

A second question that arises from the Mkomazi pattern is whether a single *Acacia* species always occupies the same daily interval, or whether this is sensitive to the set of interacting *Acacia* species in a given community. Although it is difficult or impossible to prove the cause of the observed patterns, differences within species between locations certainly do occur. In Mpala, Kenya, approximately 500 km from the Mkomazi Game Reserve, *A. nilotica* dehisces about noon, rather than just after dawn as it does in Mkomazi. In contrast, *A. brevispica* releases its pollen earlier in Mpala (about noon) than in Mkomazi (mid-afternoon) (Stone *et al.* 1998; G. N. Stone, P. G. Willmer, S. A. Whiten and A. Schnabel, unpubl. data). The fact that changes in the timing of pollen release can occur in both directions (i.e. earlier and later) argues against any simple environmental cause for these shifts in timing and is more suggestive of population-level genetic differences. It is too early to say whether the acacias at Mpala show the same evidence for resource partitioning as observed at Mkomazi.

Is resource partitioning a common feature of co-flowering acacia assemblages worldwide? Results of the work in México suggest that similar structuring occurs there (Raine 2001), but in Australian acacia assemblages there is very little evidence of the necessary synchrony of pollen release within species (M. Prescott, unpubl. data). A requirement of daily partitioning is that cues triggering pollen release change in a reliable daily pattern. In the Mkomazi community, each species dehisces over a different relative humidity range. The wide fluctuation in relative humidity in a seasonally arid habitat would be a reliable structuring mechanism, and adaptive modification of desiccation-sensitive structures in the anther would allow selective modification of the timing of pollen release. More mesic environments (such as that in which the Victoria community grows) experience both lower diurnal fluctuations in cues such as relative humidity and temperature, and more variation in climate from day to day. It is possible that the necessary structuring cues for daily partitioning do not exist in such habitats. The greater variability between days may also mean that acacias in such habitats are selected to maintain more flexible and opportunistic strategies, so that good days can be exploited when they occur.

Finally, assessment of community-level processes requires knowledge of which plant taxa interact. Interaction among acacia species is to be expected, but which other species are involved? The same arguments that allow sharing of pollinators among acacias also allow sharing with other mimosoid legumes with structurally similar flowers and visited by similar pollinators (Simpson 1977; Arroyo 1981). In some areas, the diversity of other mimosoids is low—for example, in Mkomazi the only genera in this group are *Dichrostachys* and *Albizia*. However, in Central and South America there is a far greater diversity of potentially interacting species. The Mexican acacia species listed in Table 1 are sympatric with members of at least 12 other mimosoid genera (*Acaciella, Calliandra, Desmanthus, Enterolobium, Inga, Leucana, Lysiloma, Mimosa, Neptunia, Piptadenia, Pithecellobium* and *Prosopis*) (Raine 2001) and so the web linking plants via shared pollinators may potentially extend far beyond *Acacia* (see also Simpson 1977). This makes analysis of such 'pollinator webs' (Dicks

Table 4.   Daily patterns of floral reward availability in the Mkomazi *Acacia* species (Stone *et al.* 1998)
Values given for each variable indicate the ranges within species observed across days, sites and years. Relative humidity at dehiscence
represents the mean value over the period between onset of pollen release and maximum availability

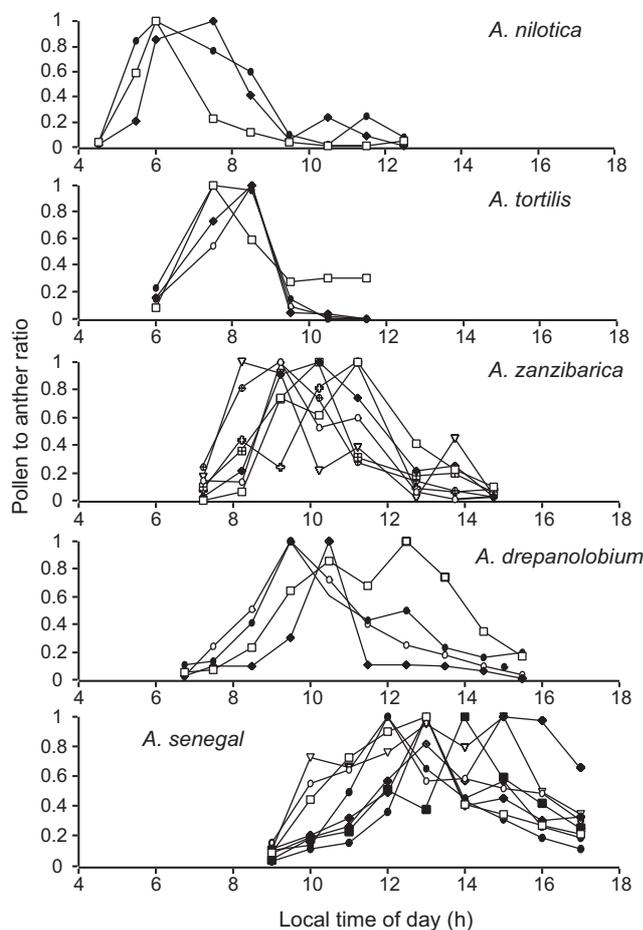| *Acacia* species	Nectar	Flowers begin to open (hours)	Dehiscence begins (hours)	Peak pollen availability (hours)	Relative humidity at dehiscence (%)
A. nilotica	None	0200–0300	0400–0500	0600–0700	90–95
A. tortilis	Trace	0400–0500	0600–0700	0730–0900	80–90
A. drepanolobium	None	0600–0700	0700–0800	1000–1200	60–70
A. zanzibarica	Trace	0700–0800	0800–0900	1000–1100	55–65
A. bussei	Present	0400–0500	0700–0800	1000–1100	65–85
A. senegal	Present	0900–1000	0900–1000	1100–1300	50–60
A. brevispica	None	1000–1100	1000–1100	1500–1600	40–50

Fig. 5. Patterns of pollen availability through time for individual trees of *Acacia nilotica*, *A. tortilis*, *A. zanzibarica*, *A. drepanolobium* and *A. senegal* in the Mkomazi Game Reserve, Tanzania. Each symbol represents an individual tree. Pollen release is scored as described for Fig. 3.

each others pollination through maintenance of larger pollinator populations than any species could alone (Waser and Real 1979; Rathcke 1983; Stone *et al.* 1998).

Ant repellents in *Acacia*

Acacias illustrate two aspects of interactions between ants and flowers—one general and the other specific to those *Acacia* species that harbour symbiotic ant guards (Hocking 1970; Janzen 1974). First, flowers in which pollen is exposed on the surface risk harvesting or chemical damage to that pollen from foraging ants (Feinsinger and Swarm 1978; Wagner 2000). Second, aggressive ant guards could potentially repel or prey on pollinators, so directly interfering with fruit set. Experimental evidence from two African ant acacias (*A. seyal* and *A. zanzibarica*) and one Mexican ant acacia (*A. hindsii*) suggests that the flowers of these plants release an ant-repellent volatile that effectively excludes ants from the flowers during dehiscence, so avoiding both potential problems (Willmer and Stone 1997; Raine *et al.* 2002; P. G. Willmer, S. G. Potts, B. Vulliamy, C. V. Nuttman and G. N. Stone, unpubl. data). Furthermore, results of experiments involving the flowers of other acacias that lack ant guards suggest that ant repellents are a general feature of acacia flowers that has been augmented in ant acacias (Ghazoul 2001; Raine *et al.* 2002). Ant guards are found in a wide taxonomic diversity of plants, including other mimosoid legume groups (e.g. *Inga*, Koptur 1984; see also Koptur 1992) and it is probable that the general points illustrated in *Acacia* will also be found in other ant–plant interactions.

Pollination and conservation

Fragmentation of natural habitats by human activity reduces native-plant populations directly through clearance, and also less obviously by damage to pollinator populations (Buchman and Nabhan 1996; Lennartsson 2002; Potts *et al.* 2003*a*, 2003*b*). Maintenance of pollinator populations must therefore be a significant component of plant-conservation efforts. This raises the following three challenges for conservation ecologists:

et al. 2002) much more challenging and may mean that demonstration of the type of pattern seen in Mkomazi is only possible in less taxonomically diverse habitats. A quantitative analysis of the importance of different plants to shared pollinators may also reveal that with or without resource partitioning, co-flowering acacias in fact facilitate

(1) Detailed observations, and preferably exclusion experiments, are required to determine which of an array of flower visitors are actually important in seed set.

(2) Once pollinators have been identified, other plants they visit must also be identified. Bees require both pollen and nectar for their brood and those visiting acacias that offer only pollen must also visit other plants for nectar. Acacias are thus embedded in a web of plants joined by their pollinators (Dicks *et al.* 2002). If the relationship between the bee and its nectar source is a specific one, then conservation of the nectar source is essential for the bee and the acacia(s) it pollinates. Plants linked by shared pollinators in this way do not compete (see above), but facilitate each other's reproduction (Bernhardt and Walker 1984; Hingston 1999).

(3) In addition to floral resources, many solitary bees in particular have highly specific requirements for nest sites, including slope, soil texture and aspect (Roubik 1989; Potts and Willmer 1997; Potts *et al.* 2003*b*). Loss of suitable nest sites will lead to pollinator decline as surely as loss of food sources.

It is entirely possible that acacias reduced to relict populations have already lost any associated specialist pollinators, with the result that seed set is now dependent on opportunist or non-specialist visitors, and likely to be lower as a result. In some cases, such as visitation of Mexican *A. hindsii* by introduced honeybees, novel pollinators may act as effective replacements for native coevolved pollinators. However, the relative merits of introduced and native pollinators have rarely been compared (but see Potts *et al.* 2003*a*, *b*), and the utility of introduced pollinators cannot be assumed. It is clear that pollinator limitation is already an issue for endangered acacias in Australia, particularly those restricted to roadside strips of remnant vegetation in the south-western wheatbelt (*A. brachybotrya*, Cunningham 2000*a*, 2000*b*; *A. aprica* and *A. cochlocarpa* subsp. *cochlocarpa*, M. Prescott, unpubl. data).

The discussion of competition for pollination above also highlights the fact that introduced mimosoid legumes may constitute a significant threat to endemic acacias (and other mimosoids). The type of interaction described above for *A. pycnantha* and *A. myrtifolia* (Bernhardt and Walker 1984) could, for example, apply equally to the impact of *Acacia nilotica* (or invading mimosa) on the pollination of Australian acacias. Introduced Australian acacias could potentially have a similar detrimental impact on native acacias in southern Africa. This issue is urgently in need of further study.

Acknowledgements

References

Ali SL, Quaiser M (1980) Hybridisation in the *Acacia nilotica* (Mimosoideae) complex. *Botanical Journal of the Linnean Society* **80**, 69–77.

Alvarez T, Gonzalez Quintero (1969) Análisis polínico del contenido gastricode murcielágos Glossophaginae de México. *Annales de la Escuela Nacional de Ciencias Biologicas de México* **18**, 137–165.

Alvarez T, Sanchez-Casas N (1999) Sexual diet differences in *Glossophaga soricina* (Chiroptera: Phyllostomidae) from Mexico. *Revista de Biologia Tropical* **47**, 1129–1136.

Armstrong JA (1979) Biotic pollination mechanisms in the Australian flora—a review. *New Zealand Journal of Botany* **17**, 467–508.

Arroyo MTK (1981) Breeding systems and pollination biology in Leguminosae. In 'Advances in legume systematics'. (Eds RM Polhill, PH Raven) pp. 723–769. (Royal Botanic Gardens Kew: Richmond, Surrey, UK)

Baranelli JL, Cocucci AA, Anton AM (1995) Reproductive biology in *Acacia caven* (Mol.) Mol. (Leguminosae) in the central region of Argentina. *Biological Journal of the Linnean Society* **119**, 65–76.

Beentje H (1994) 'Kenya trees shrubs and lianas.' (National Museums of Kenya: Nairobi, Kenya)

Bernhardt P (1983) Insect pollination of Australian acacias. In 'Pollination 82'. (Eds EG William, RB Knox, JH Gilbert, P Bernhardt) pp. 85–101. (University of Melbourne)

Bernhardt P (1987) A comparison of the diversity, density and foraging behaviour of bees and wasps on Australian *Acacia*. *Annals of the Missouri Botanical Garden* **74**, 42–50.

Bernhardt P (1989) Floral ecology of Australian acacias. In 'Advances in legume biology'. Monograph in systematic botany from the Missouri Botanical Garden, no. 29. (Eds CH Stirton, JL Zaruchi) pp. 263–282. (Missouri Botanical Garden: St Louis, MI)

Bernhardt P, Kenrick J, Knox RB (1984) Pollination biology and the breeding system of *Acacia retinodes* (Leguminosae: Mimosoideae). *Annals of the Missouri Botanical Garden* **71**, 17–29.

Bernhardt P, Walker K (1984) Bee foraging on three sympatric species of Australian *Acacia*. *International Journal of Entomology* **26**, 322–330.

Bernhardt P, Walker K (1985) Insect foraging on *Acacia retinodes* var. *retinodes* in Victoria, Australia. *International Journal of Entomology* **27**, 97–101.

Buchman S, Nabhan SL (1996) 'The forgotten pollinators.' (Island Press/Shearwater Books: Washington, DC)

Chappill JA, Maslin BR (1995) A phylogenetic assessment of the tribe Acacieae. In 'Advances in legume systematics, vol. 7—Phylogeny'. (Eds M Crisp, JJ Doyle) pp. 77–99. (Royal Botanic Gardens Kew: Richmond, Surrey, UK)

Coe MJ, McWilliam NC, Stone GN, Packer MJ (1999) (Eds) 'Mkomazi: the ecology, biodiversity and conservation of a Tanzanian savanna.' (Royal Geographical Society: London)

Cunningham SA (2000*a*) Depressed pollination in habitat fragments causes low fruit set. *Proceedings of the Royal Society of London B Biological Sciences* **1448**, 1149–1152.

Cunningham SA (2000*b*) Effects of habitat fragmentation on the reproductive ecology of four plant species in mallee woodland. *Conservation Biology* **14**, 758–768.

Diallo I, Samb PI, Gaye A, Sall PN, Duhoux E, Ba AT (1997) Floral biology and pollination in *Acacia senegal* (L.) Wild. *Acta Botanica Gallica* **144**, 73–82.

Dicks LV, Corbet SA, Pywell RF (2002) Compartmentalization in plant–insect flower visitor webs. *Journal of Animal Ecology* **71**, 32–43.

Dutoit JT (1990) Giraffe feeding on acacia flowers—predation or pollination? *African Journal of Ecology* **28**, 63–68.

Feinsinger P, Swarm LA (1978). How common are ant-repellent nectars? *Biotropica* **10**, 238–239.

Fishbein M, Venable DL (1996) Diversity and Temporal change in the effective pollinators of *Asclepias tuberosa*. *Ecology* **77**, 1061–1073.

Ford HA, Forde N (1976) Birds as possible pollinators of *Acacia pycnantha*. *Australian Journal of Botany* **24**, 793–795.

Friedel MH, Nelson DJ, Sparrow AD, Kinloch JE, Maconochie JR (1994) Flowering and fruiting of arid zone species of *Acacia* in Central Australia. *Journal of Arid Environments* **27**, 221–239.

Ghazoul J (2001) Can floral repellents pre-empt potential ant–plant conflicts? *Ecology Letters* **4**, 1–5.

Gilbert FS (1981) Foraging ecology of hoverflies: morphology of the mouthparts in relation to feeding on nectar and pollen in some common urban species. *Ecological Entomology* **6**, 245–262.

Hagerup O (1932) On pollination in the extremely hot air of Timbuktu. *Dansk Botanisk Archiv* **8**, 1–20.

Heinrich B, Heinrich MJE (1983) Heterothermia in foraging workers and drones of the bumblebee, *Bombus terricola*. *Physiological Zoology* **56**, 563–567.

Hingston AB (1999) Affinities between southern Tasmanian plants in native visitor profiles. *Australian Journal of Zoology* **47**, 361–384.

Hocking B (1970) Insect associations with the swollen thorn *Acacia* species. *Transactions of the Royal Entomological Society of London* **122**, 211–255.

Hopkins MS, Graham AW (1989) Community phenology patterns of a lowland tropical rainforest in north-eastern Australia. *Australian Journal of Ecology* **14**, 399–413.

Horvitz CC, Schemske DW (1988) A test of the pollinator limitation hypothesis for a neotropical herb. *Ecology* **69**, 200–206.

Janzen DH (1966) Coevolution of mutualism between ants and acacias in Central America. *Evolution* **20**, 249–275.

Janzen DH (1967) Interaction of the bull's horn *Acacia* (*Acacia cornigera* L.) with an ant inhabitant (*Pseudomyrmex ferruginea* F.Smith) in Eastern Mexico. *University of Kansas Science Bulletin* **157**, 315–558.

Janzen DH (1974) Swollen-thorn acacias of Central America. *Smithsonian Contributions to Botany* **13**, 1–131.

Kenrick J (2003) Review of pollen-pistil interactions and their relevance to reproductive biology of *Acacia*. *Australian Systematic Botany* **16**, 119–130.

Kenrick J, Knox RB (1982) Function of the polyad in reproduction of *Acacia*. *Annals of Botany* **50**, 721–727.

Kenrick J, Knox RB (1989) Pollen-Pistil interactions in Leguminosae (Mimosoideae) In 'Advances in legume biology'. Monograph in systematic botany from the Missouri Botanical Garden, no. 29. (Eds CH Stirton, JL Zaruchi) pp. 127–156. (Missouri Botanical Garden: St Louis, MI)

Kenrick J, Bernhardt P, Marginson R, Beresford G, Knox RB, Baker I, Baker HG (1987). Pollination-related characteristics in the mimosoid legume *Acacia terminalis*. *Plant Systematics and Evolution* **157**, 49–62.

Knox RB, Kenrick J, Bernhardt P, Marginson R, Beresford G, Baker I, Baker HG (1985) Extrafloral nectaries as adaptations for bird pollination in *Acacia terminalis*. *American Journal of Botany* **72**, 1185–1196.

Koptur S (1984) Experimental evidence for defense of *Inga* (Mimosaceae) saplings by ants. *Ecology* **65**, 1787–1793.

Koptur S (1992) Extrafloral nectary-mediated interactions between insects and plants. In 'Insect–plant interactions'. (Ed. EA Bernays) pp. 81–129. (CRC Press: Boca Raton, FL)

Krüger O, McGavin GC (1998) The insect fauna of *Acacia* species in Mkomazi Game Reserve, north east Tanzania. *Ecological Entomology* **22**, 440–444.

Larsen TB (1991) 'The butterflies of Kenya and their natural history.' (Oxford University Press: Oxford, UK)

Leach GJ, Whiffin FLS (1978) Analysis of a hybrid swarm between *Acacia brachybotrya* and *A. calamifolia* (Leguminosae). *Botanical Journal of the Linnean Society* **76**, 53–69.

Lennartsson T (2002) Extinction thresholds and disrupted plant-pollinator interactions in fragmented plant populations. *Evolution* **83**, 3060–3072.

Maslin B (2001) 'Mimosaceae, *Acacia*. Flora of Australia, vols 11A, B.' (ABRS/CSIRO Publishing: Melbourne)

Maslin B, Pedley L (1982) The distribution of *Acacia* (Leguminosae: Mimosoideae) in Australia. Part 2. Lists of species occurring in 1 × 5° grid cells. *Western Australian Herbarium Research Notes* **6**, 129–171.

Midgely SJ, Turnbull JW (2003) Domestication and use of Australian acacias: case studies of five important species. *Australian Systematic Botany* **16**, 89–102.

Miller JT, Bayer RJ (2001) Molecular phylogenetics of *Acacia* (Fabaceae, Mimosoideae) based on the chloroplast MATK coding region and flanking TRNK intron spacer regions. *American Journal of Botany* **88**, 697–705.

Milton SJ (1987) Phenology of seven *Acacia* species in South Africa. *South African Journal of Wildlife Research* **17**, 1–6

Milton SJ, Moll EJ (1982) Phenology of Australian acacias in the SW Cape, South Africa, and its implications for management. *Botanical Journal of the Linnean Society* **84**, 295–327.

Morgan A, Carthew SM, Sedgley M (2002) Breeding system, reproductive efficiency and weed potential of *Acacia baileyana*. *Australian Journal of Botany* **50**, 357–364.

Mosquin T (1971) Competition for pollinators as a stimulus for the evolution of flowering time. *Oikos* **22**, 398–402.

Noort S van, Stone GN (1999) Butterflies (Lepidoptera: Hesperioidea and Papilionoidea) of Mkomazi. In 'Mkomazi, the ecology, biodiversity and conservation of a Tanzanian savanna'. (Eds MJ Coe, N McWilliam, GN Stone, M Packer) pp. 281–298. (The Royal Geographical Society: London)

Paynter Q, Csurhes SM, Heard TA, Ireson J, Julien MH, Lloyd J, Lonsdale WM, Palmer WA, Sheppard AW, van Klinken RD (2003) Worth the risk? Introduction of legumes can cause more harm than good: an Australian perspective. *Australian Systematic Botany* **16**, 81–88.

Peralta I, Rodriguez JG, Arroyo MTK (1992) Breeding system and aspects of pollination in *Acacia caven* (Mol.) Mol. (Leguminosae: Mimosoideae) in the Mediterranean-type climate zone of central Chile. *Botanische Jarbücher für Systematik Pflanzengeschichte und Pflanzengeographie* **114**, 297–314.

Pleasants JM (1980) Competition for bumblebee pollinators in Rocky Mountain plant communities. *Ecology* **61**, 1446–1459.

Poole RW, Rathcke BJ (1979) Regularity, randomness and aggregation in flowering phenologies. *Science* **203**, 470–471.

Potts SG, Willmer P (1997) Abiotic and biotic factors influencing nest-site selection by *Halictus rubicundus*, a ground-nesting halictine bee. *Ecological Entomology* **22**, 319–328.

Potts SG, Vulliamy B, Dafni A, O'Toole C, Roberts S, Willmer PG (2003*a*) Response of plant–pollinator communities following fire: changes in diversity, abundance and reward structure. *Oikos* in press.

Potts SG, Vulliamy B, Dafni A, Ne'eman G, Willmer PG. (2003*b*) Linking bees and flowers: how do floral communities structure pollinator communities? *Ecology* in press.

Radford IJ, Nicholas M, Tiver F, Brown J, Kriticos D (2002) Seedling establishment, mortality, tree growth rates and vigour of *Acacia nilotica* in different *Astrebla* grassland habitats: implications for invasion. *Australian Ecology* **27**, 258–268.

Raine NE (2001) The pollination ecology of a Mexican *Acacia* community. PhD Thesis, University of Oxford, UK.

Raine NE, Willmer PG, Stone GN (2002) Spatial structuring and floral avoidance behaviour prevent ant–pollinator conflict in a Mexican ant-acacia. *Ecology* **83**, 3086–3096.

Rathcke B (1983) Competition and Facilitation among plants for pollination. In 'Pollination biology'. (Ed. L Real) pp. 305–329. (Academic Press: New York)

Rathcke B (1988) Flowering phenologies in a shrub community: competition and constraints. *Journal of Ecology* **76**, 975–994.

Robinson J, Harris SA (2000) A plastid DNA phylogeny of the genus *Acacia* Miller (Acacieae, Leguminosae). *Botanical Journal of the Linnean Society* **132**, 195–222.

Ross JH (1981) An analysis of the African *Acacia* species: their distribution, possible origins and relationships. *Bothalia* **13**, 389–413.

Roubik DW (1989) 'Ecology and natural history of tropical bees.' (Cambridge University Press: Cambridge, UK)

Roxburgh L, Pinshow B (2000) Nitrogen requirements of an old world nectarivore, the orange-tufted sunbird *Nectarinia osea*. *Physiological and Biochemical Zoology* **73**, 638–645.

Sedgley M (1989) *Acacia*. In 'Handbook of flowering'. (Ed. AH Halevy) pp. 1–11. (CRC Press: Boca Raton, FL)

Sedgley M, Harbard J (1993) Pollen storage and breeding system in relation to controlled pollination of four species of *Acacia* (Leguminosae, Mimosoideae). *Australian Journal of Botany* **40**, 601–609.

Sedgley M, Harbard J, Smith R-MM, Wickneswari R, Griffin AR (1992) Reproductive biology and interspecific hybridisation of *Acacia mangium* and *Acacia auriculiformis* A.Cunn. ex Benth. (Leguminosae: Mimosaceae). *Australian Journal of Botany* **40**, 37–48.

Simpson B (1977) Breeding systems of dominant perennial plants in two disjunct warm desert ecosystems. *Oecologia* (*Berlin*) **27**, 203–336.

Sornsathapornkul P, Owens JN (1998) Pollination biology in a tropical *Acacia* hybrid (*A. mangium* Willd. × *A. auriculiformis* A.Cunn. ex Benth). *Annals of Botany* **81**, 631–645.

Stone GN, Willmer PG, Nee S (1996) Daily partitioning of pollinators in an *Acacia* community. *Proceedings of the Royal Society B*, **263**, 1389–1393.

Stone GN, Willmer PG, Rowe JA (1998) Partitioning of pollinators during flowering in an African *Acacia* community. *Ecology* **79**, 2808–2827.

Stone GN, Willmer PG, Rowe JA, Nyundo B, Abdallah R (1999) The pollination ecology of Mkomazi *Acacia* species. In 'Mkomazi, the ecology, biodiversity and conservation of a Tanzanian savanna'. (Eds MJ Coe, N McWilliam, GN Stone, M Packer) pp. 337–360. (The Royal Geographical Society: London)

Tandon R, Shivanna KR, Mohan Ram HY (2001) Pollination biology and breeding system of *Acacia senegal*. *Botanical Journal of the Linnean Society* **135**, 251–262.

Tets IG van, Nicolson SW (2000) Pollen and the nitrogen requirements of the lesser double-collared sunbird. *Auk* **117**, 826–830.

Turnbull JW (1987) (Ed.) 'Australian acacias in developing countries.' *Australian Centre for International Agricultural Research Proceedings* **16** (ACIAR, Canberra).

Tybirk K (1989) Flowering, pollination and seed production of *Acacia nilotica*. *Nordic Journal of Botany* **9**, 375–381.

Tybirk K (1993) Pollination, breeding system and seed abortion in some African *Acacia* species. *Botanic Journal of the Linnean Society* **112**, 107–137.

Vanstone VA, Paton DC (1988) Extrafloral nectaries and pollination of *Acacia pycnantha* by birds. *Australian Journal of Botany* **36**, 519–531.

Wagner D (2000) Pollen viability reduction as a potential cost of ant association for *Acacia constricta* (Fabaceae). *American Journal of Botany* **87**, 711–715.

Waser NM (1978*a*) Competition for hummingbird pollination and sequential flowering in two Colorado wildflowers. *Ecology* **59**, 934–944.

Waser NM (1978*b*) Interspecific pollen transfer and competition between co-occurring plant species. *Oecologia* (*Berlin*) **36**, 223–236.

Waser NM (1983) Competition for pollination and floral character differences among sympatric plant species: a review of the evidence. In 'Handbook of experimental pollination biology'. (Eds CE Jones, RJ Little) pp. 277–293. (Van Nostrand Reinhold: New York)

Waser NM, Fugate ML (1986) Pollen precedence and stigma closure: a mechanism of competition for pollination between *Delphinium nelsonii* and *Ipomopsis aggregata*. *Oecologia* (*Berlin*) **70**, 573–577.

Waser NM, Real LA (1979) Effective mutualism between sequentially flowering plant species. *Nature* **281**, 670–672.

Williams MR (1995) Critical values of a statistic to detect competitive displacement. *Ecology* **76**, 646–647.

Willmer PG, Stone GN (1997) Ant deterrence in *Acacia* flowers: how aggressive ant-guards assist seed-set. *Nature* **388**, 165–167.

Zapata TR, Arroyo MTK (1978) Plant reproductive ecology of a secondary deciduous forest in Venezuela. *Biotropica* **10**, 221–230.