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Flower color phenology in European grassland and woodland habitats, through the eyes of pollinators

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ABSTRACT

Some studies have claimed that flowers in bloom at particular times of year are more likely to be of particular colors to better attract pollinating insects. To test this, we analyzed a data set collected from five field sites near Strausberg, Germany, which included information on flower color and months of blooming. However, we chose to consider flower color as perceived by bee as well as human visual systems, as well as independent of any color vision system, to reveal whether trends, if present, have any ecological relevance. Using randomization analyses, we were able to consider whether blooming time interacts with flower color, and how this interaction depends upon other factors. Our results show that there is an association between the months of flowering and the colors of flowers—but only when flowers are considered according to human color categories. Further analysis showed that this is merely a consequence of flowers from the same family being more likely to flower at the same time and have similar colors. All these effects disappeared when flowers were considered using bee color categories, and in the analyses of physical spectral reflectances.

Keywords: bee vision, color space, flower pigment, pollination syndrome, sensory ecology

INTRODUCTION

There have been many observations about the colors of flowers that are present at different times of year. Robertson (1924), for example, stated that greenish-yellow flower species tend to bloom earlier in the year than other colors; McCann (1986) claims that spring flowers are most frequently white, and late summer flowers more likely to be yellow; Warren and Billington (2005) conclude that there is a significant interaction between flower color and month, stating that yellow, white, and pink/purple flowers are all most abundant in early summer, while blue flowers are more or less constant in abundance throughout the flowering season. However, relatively little work has been done to analyze this aspect of phenology statistically, and none at all that considers the flowers' colors as their pollinators see them rather than relying on human classifications, which might be of limited ecological relevance. In this study, we have chosen to analyze the flowers classified by the colors as they appear to the most significant pollinators in the local habitat: bee species (including honeybees, *Apis mellifera*, bumblebees, *Bombus* spp., and diverse solitary bees). We have also considered the colors of flowers based on their spectral properties, independently of any visual system.

Flowering plant species can reduce competition for pollinators via a number of methods, including separation of flowering in time or space from other species, and evolving a different color to its neighbors to make the species easier to discriminate by the pollinator and thus secure more conspecific pollen (Heinrich, 1975; Waser, 1978, 1983; Rathcke, 1983; Rathcke and Lacey,

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1985). However, there is also a trade-off: flowering as part of a large group can attract more pollinators because of a mass display effect (Heinrich, 1975). Therefore the flower has to balance being visually distinct or physically separate from other species against being too separate and not attracting sufficient pollinators. With regard to phenology, this is reflected in two contrasting hypotheses that predict how biotically pollinated flowers should time their blooming relative to other species in the community. First, it has been suggested that by staggering flowering times, plants can minimize interspecific competition for pollinators and so all species will benefit; secondly, that by synchronizing flowering times, all the species will benefit by attracting more pollinators with a mass display effect (Rathcke and Lacey, 1985) (see Martínková et al., 2002, for an overview).

What is often overlooked, however, is the interaction between phenology and the colors of the flowers; it may not be necessary for two flower species to diverge in flowering time if they are of different colors and therefore easily distinguished by pollinators. Many species of pollinators have excellent color vision and are therefore able to discriminate flowers of different colors with great accuracy (Frisch, 1914; Menzel, 1985b; Kevan and Backhaus, 1998; Briscoe and Chittka, 2001; Kelber et al., 2003; Internicola et al., 2008). The color vision of Hymenoptera is well understood and modeled (Frisch, 1914; Daumer, 1958; Menzel, 1975; Menzel, 1985a; Backhaus, 1991; Chittka et al., 1992). Given their good color vision, the color preferences of pollinating insects can act as an important selective force in the appearance of entomophilous flowers.

Flowers might thus be under selective pressure both to display the color that is most attractive to their principal pollinator, and to flower at the time of year that will attract that pollinator type in the largest numbers. This relates to the pollination syndrome hypothesis, which holds that a certain suite of features (including color and shape) is associated specifically with a particular guild of pollinators (Faegri and van der Pijl, 1978). For example, some solitary bees and certain species of bumblebee (especially newly-emerged queens) are most active in early spring (Heinrich, 1976; Macior, 1978; Herrera, 1988). Therefore, one might expect there to be selection for those flowers that bloom around this time to be maximally attractive to bees by producing pigments in "bee colors"—typically blue/violet to human eyes, or blue (with or without UV reflectance) according to bee perception. By comparison, later in the season more butterflies and hoverflies are active (Herrera, 1988; Bosch et al., 1997; Gutiérrez and Menéndez, 1998), perhaps leading one to expect more of an abundance of the pink/purple flowers considered to be preferred by butterflies, and the white and yellow ones that are visited by many syrphids (hoverflies) (Lunau and Maier, 1995). Such flowers may typically appear UV-blue in the case of "butterfly" flowers, and blue-green and green in the case of "fly" flowers, when modelled in bee color space.

However, despite the predictions of the pollination syndrome hypothesis that pollinating insects will be instinctively drawn to flowers exhibiting particular characteristics such as certain colors, it is well known that insects are plastic in their behavior. Indeed, there is abundant evidence that many are excellent learners (Menzel, 1985b; Kelber, 1996; Gumbert, 2000; Chittka and Raine, 2006; Zaccardi et al., 2006), able to associate almost any color with reward. They can therefore potentially take advantage of all the colors of rewarding flowers available in a habitat at a given time. Thus, there may only be minimal advantage to displaying colors preferred innately by the dominant pollinator group at a certain time of year. A better strategy may be to evolve a distinctive color, to reduce the number of transitions between plant species by foraging pollinators and ensure the conspecificity of pollen (Gumbert et al., 1999).

It is important not to neglect the previous observations that flowering characteristics can be affected simply by the plant's evolutionary history. For example, one of the most important predictors of flowering phenology may simply be the family of the plant (Ollerton and Lack, 1992; Fox and Kelly, 1993). This may not necessarily be an evolutionary constraint per se, but certainly some clades seem to have a tendency to flower at similar times of year (e.g., the Asteraceae typically flower later in the year (Ollerton and Lack, 1992)). It has also been noted that some families (e.g., Apiaceae) have a large number of flowers of broadly similar colors (Chittka et al., 1994; Chittka, 1997). This means that any study of this type needs to take such potential correlations into account. Additionally, some particular locations have strongly skewed distributions of flower color (Kevan and Baker, 1983; Goldblatt et al., 1998), so it is important to consider the potential influence of habitat in our analysis.

In this study, we investigated whether flowers of particular colors (as seen by bees as well as by human observers, and also considered according to their physical reflectance spectra) tend to bloom at particular times of year. Such a finding might indicate an evolutionary adaptation to a particular guild of pollinators. Alternatively, in a given habitat, flowers of all colors may bloom throughout the year. This observation would instead lend support to the theory that pollination is a market in which flowers compete against one another for pollinators and therefore are under pressure to be different, distinctive, and salient, more than fulfilling a particular suite of predefined characteristics that are considered to make them best-suited to a certain pollinator species (Heinrich, 1979; Peleg et al., 1992; Waser et al., 1996; Ollerton et al., 2009).

MATERIALS AND METHODS

Study site and data collection

The data were collected from Unteres Annatal-Lange Dammwiesen, a nature reserve located near Strausberg in Brandenburg, Germany, during 1991–1993. Five ecologically distinct sites were studied at this location, each ca. 500 m^2 in area, referred to in this article as "dry grassland", "humid meadow", "roadside", "maple shrub", "hazel woodland". The study sites were visited fortnightly between March and October each year, and any insect-visited flowering species in bloom were recorded. Additionally, spectral reflectance readings were taken of all the flower species using a flash spectrophotometer (using a protocol as in Menzel and Shmida, 1993; Gumbert et al., 1999; see also Chittka and Kevan, 2005). This produces a data set for each species consisting of the proportion of total light reflected by the flower surface at each wavelength in the bee visible range (300–700 nm), at 1 nm intervals.

In total, we collected observations for 146 species from 30 plant families. Some species occurred in more than one habitat, while others occurred in only a single habitat. Colors and flowering times of all species observed are included in Appendices, and are the same as those given in Gumbert et al. (1999). Spectral reflectance data for all species can be found online in the Floral Reflectance Database (http://www.reflectance.co.uk) (Arnold et al., 2008).

Color categories

Bees (including solitary species such as *Lasioglossum*, and several *Bombus* species) are usually the principal pollinators in these types of habitats in Germany (Steffan-Dewenter and Tscharntke, 1999; Steffan-Dewenter et al., 2002; Raine and Chittka, 2007). However, other pollinators present include syrphids, beetles, and butterflies (Kunze and Chittka, 1996; Waser et al., 1996; Steffan-Dewenter and Tscharntke, 1999). As honeybees and bumblebee species have been shown to have broadly similar color vision (Peitsch et al., 1992; Briscoe and Chittka, 2001), we calculated flower color loci as viewed by a honeybee, using the color hexagon model and the methodology described in Chittka (1992) and Gumbert et al. (1999). We are only beginning to understand how bees categorize color (Benard and Giurfa, 2008); however, the bee color hexagon can be divided into six segments and these can be regarded as operational color categories, as in Fig. 1. Previous research (Chittka et al., 1994) has shown that flower colors' loci tend to fall towards the center of these categories, so it would appear to be a useful way to group bee colors. Indeed, our data show the same trend, with the largest numbers of loci falling at 60-degree intervals around the hexagon, corresponding to the centers of categories.

The loci of all the points used in this analysis are also shown in Fig. 1. The "bee color categories" classify colors differently from human evaluations; flowers that appear yellow to a human can appear either green or UV-green to a bee depending on the ultraviolet component (as they stimulate the bee's long-wavelength receptor, maximally sensitive to green light and, depending on their short-wavelength reflectance, possibly also the UV receptor), while both human-white and -pink flowers may appear blue-green to a bee (as these flowers usually reflect wavelengths between what humans would term blue and green, and absorb ultraviolet) (Chittka et al., 1994).

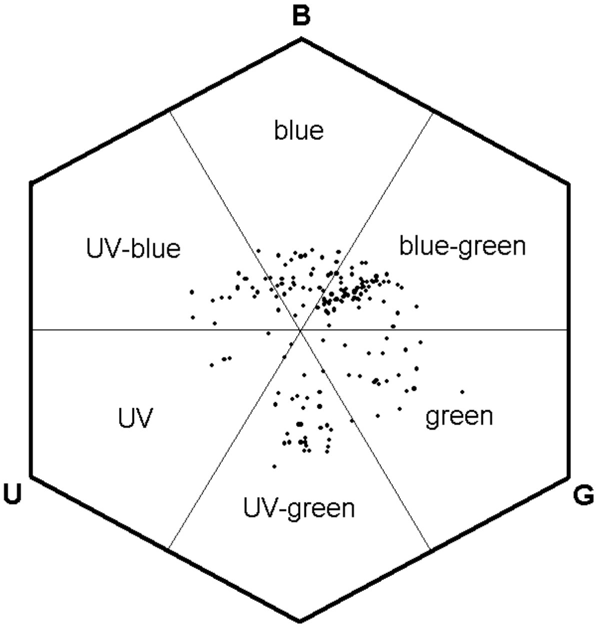

Fig. 1. Bee color hexagon with loci of sample flower species plotted. Bees typically have three photoreceptor types, sensitive to UV, blue, and green light. Loci of individual flower colors are shown as points. The receptor signals are determined for the flowers of each plant species; the relative strength of the signals for each species is expressed as the proximity of the locus to the labeled apices of the hexagon. The hexagon can then be divided into segments, each one corresponding to a different color category. The most common bee color for these flowers is blue-green.

Statistical analysis: Bee and human colors

Each of the species sampled in the data set was assigned to a color category based on the appearance of its flowers, either to humans (blue, green, pink, purple, red, white, yellow) or to bees (blue, blue-green, green, UV, UV-blue, or UV-green). The same species were then categorized as flowering or non-flowering for each month between March and October. Using these data, each species in the data set was compared pairwise with each other species for each month, and the number of cases in which species of the same color group flowered in the same month was calculated. To test whether this number was greater than would be expected by chance, we elected to use a randomization approach similar to that described in Rossiter et al. (2005): flower colors were randomly reassigned within habitat and family using Mathematica 5.0 (2003) (Wolfram Research, Inc., Champaign, Illinois, USA). For each randomization, the number of cases in which species of the same color group flowered in the same month ($N_\cap$) was recalculated for the randomized data. This was repeated 10,000 times, giving a distribution of values to which $N_\cap$ could be compared; the proportion of times in which the randomized values equalled or exceeded $N_\cap$ is the p value**.** The analysis was repeated with the flower species classified according to human and bee categories, enabling us to ascertain whether there is a difference in flowering patterns depending on the visual system perceiving them.

Our statistical approach gave us the options to control for habitat and family, ensuring that ecological and phylogenetic information are preserved and accounted for as necessary. We ran randomizations both with species pooled between habitats, but families still controlled for, and with species pooled between plant families, but with habitats controlled for. We also considered each habitat individually, to ascertain whether there were trends present in some habitats but not others.

Statistical analysis: Spectral properties independent of a visual system

We also considered the flower species' colors independent of any visual processing, human or insect. This could indicate any trends in flower colors that were dictated by abiotic constraints, such as drought-tolerance in the height of summer. For the first analysis, we took the raw reflectance spectra of the species present, with all the reflectance values at 25 nm intervals between 300 and 700 nm. As flower reflectance spectra tend to change smoothly with wavelength (Chittka et al., 1994), there is little information lost by sampling at a lower wavelength interval than the original spectrophotometer measurements. This provided 17 measurements across the bee visible range for each species, which could be analyzed using Principal Components Analysis (PCA) in SPSS for Windows to extract the first two principal components describing variation between the spectra. This was done both for all habitats pooled and for each habitat individually. We divided the species into three groups of broadly similar size (in terms of number of flower species): "early" (blooming in March to May), "mid" (blooming in June and July), and "late" (blooming in August to October) in order to compare whether the flower communities at different times of year had similar compositions of spectra present. We chose to use a smaller number of flowering-time groups for this analysis compared to the month-by-month considerations of flowers in bloom for previous analyses because most species bloom in more than one month successively. Comparing the distribution of points (corresponding to flower colors for groups of species) between two consecutive months would cause pseudo-replication and the groups certainly could not be considered to be independent. As the same species has the same color in every month of flowering, many of the data points would be the same between months and therefore the chances of finding any significant difference between floral communities in consecutive months would be low.

Several flower species even occur in more than one of our broader categories, so it must be acknowledged that the groups are still not entirely independent; however, the analysis can nonetheless indicate whether there are marked changes in the variety of spectral types present in each community at different times of year.

Additionally, we considered whether the differences in phenology between flower species correlate with differences in flower color, as defined by spectral properties. To do this, we created two matrices in SPSS. The first consisted of the Euclidean distances describing the differences between the flower species' reflectance spectra. This was calculated using the spectral reflectance data at 25 nm intervals, as for the PCA.

We also calculated a dissimilarity matrix according to the differences between phenological properties of the flower species. To do this, each flower species was designated as flowering or non-flowering for each month, and the patterns of flowering were compared pairwise between species, with 1 signifying complete synchrony and 0 signifying complete asynchrony of flowering times. Using the R statistical package (R Development Core Team, 2004), we ran a Mantel test to compare the two matrices. If flowers with similar spectral properties also share similar phenological characteristics, a significant correlation between the two matrices would be observed.

RESULTS

The months in which the largest numbers of plant species flowered were June and September (Figs. 2 and 3). In the woodland habitats (hazel shrub and maple woodland), flowers generally appeared earlier (Figs. 4 and 5), with species blooming in March and/or April comprising 19.2% and 16.7% of total species, respectively, (compared to 4.7%, 0%, and 11.5%, for dry grassland, humid meadow and roadside habitats, respectively).

As in previous studies (Chittka et al., 1994), the most common bee flower color category was blue-green to bees (typically, but not always, corresponding to human white or pink) and relatively few species are bee-UV (often UV-reflecting red or orange to human eyes, such as the poppy *Papaver rhoeas* L.). White and yellow were the commonest colors when the data set was categorized by human color appearance. A first inspection of the proportions of colors as perceived by humans over the year might give the impression of substantial changes from early to later months. In March (and to a lesser extent in April), purple flower species appear much more abundant than in later months (Fig. 2, bottom), while white flower species appear less commonly in these early months. However, it is important to note that very few plant species bloom so early in the year, so the proportions of colors in early months are based on only a small number of species. From May to later months the proportions of different human colors appear largely constant (Fig. 2, bottom).

Human color categories

Our analysis revealed that despite the lower sample sizes in the early months (Fig. 2, top), the overall changes in proportions of human colors throughout the year are significant ($p = 0.048$); i.e., species in bloom in the same month are superficially likely to share the same human color.

However, when plant family was controlled for, this apparent trend disappeared ($p = 0.2784$), indicating that the recorded trend occurs only because plants in the same family tend to have similar traits (color, as perceived by humans, and flowering time). The trend also disappeared when flower colors were randomized within but not between habitats, controlling for effects of habitat on the dataset ($p = 0.1512$).

Bee color categories

For bee colors, likewise, there appears to be a change in relative color frequencies from early to late months (Fig. 3, bottom); in March, UV-blue flower species appear to be more common than in later months, whereas bee green and blue-green flowers appear less common. However, inspection of the sample sizes in the absolute counts (Fig. 3, top) once again shows that these apparent temporal changes in flower color proportions are the result of small sample sizes: there are only half a dozen species that flower in March, in all habitats taken together.

Accordingly, our randomization approach generated a result that missed the significance threshold ($p = 0.0935$), indicating no significant tendency for flowers blooming at the same time to share the same bee color, and this marginal effect vanished entirely when plant family membership was taken into account ($p = 0.2608$), or when the different habitats were controlled for ($p = 0.3099$). These findings indicate that flowering time cannot be taken as a significant predictor of bee flower color, regardless of whether or not the phylogeny of the plants in these habitats is taken under consideration.

Individual habitats

The color distributions for each habitat are shown in Figs. 4 (human colors) and 5 (bee colors). We analyzed each habitat separately with the randomization, once more controlling for possible effects of phylogeny. Regardless of whether the flower colors used were those perceived by bees or humans, no individual habitat showed a significant pattern (Table 1). Therefore, whichever of the habitats is considered, the chances of flower species in bloom in a given month being the same color to bee or human observers is no greater than chance.

Spectral properties independent of visual system

The Principal Components Analyses, both for the species from all habitats pooled and for the species in each habitat individually, are shown in Fig. 6. There appears to be a high degree of overlap between the spectral properties of species blooming at different times of

Table 1

Summary of *p*-values for the randomization tests performed on flower color trends in individual habitats. The values are the results of randomization tests investigating whether species in each habitat that share the same color also share the same flowering phenology. Randomization tests include a control for evolutionary history

Habitat	*p*-value for bee color model	*p*-value for human color model
Dry grassland	0.2239	0.2886
Humid meadow	0.5943	0.4462
Roadside	0.3057	0.6834
Hazel shrub	0.8566	0.3780
Maple woodland	0.7201	0.7588

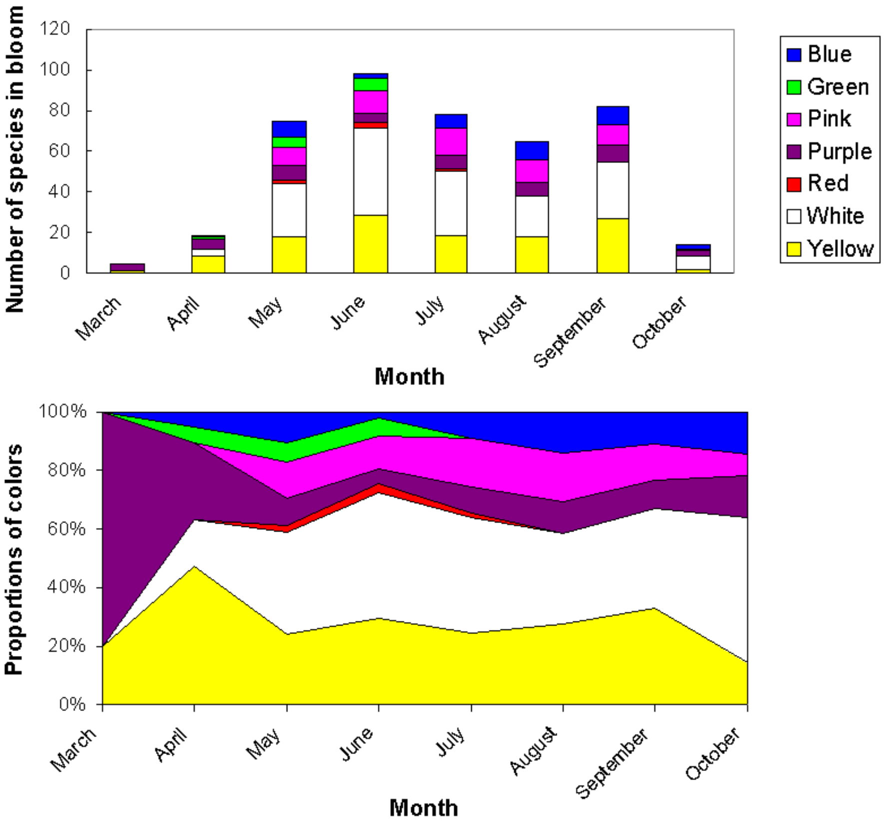

Fig. 2. Human color distributions for all sites combined. Flower species are categorized into color groups according to human judgment. The upper graph shows the absolute counts of species in bloom for all months, while the lower shows the proportions of different colors.

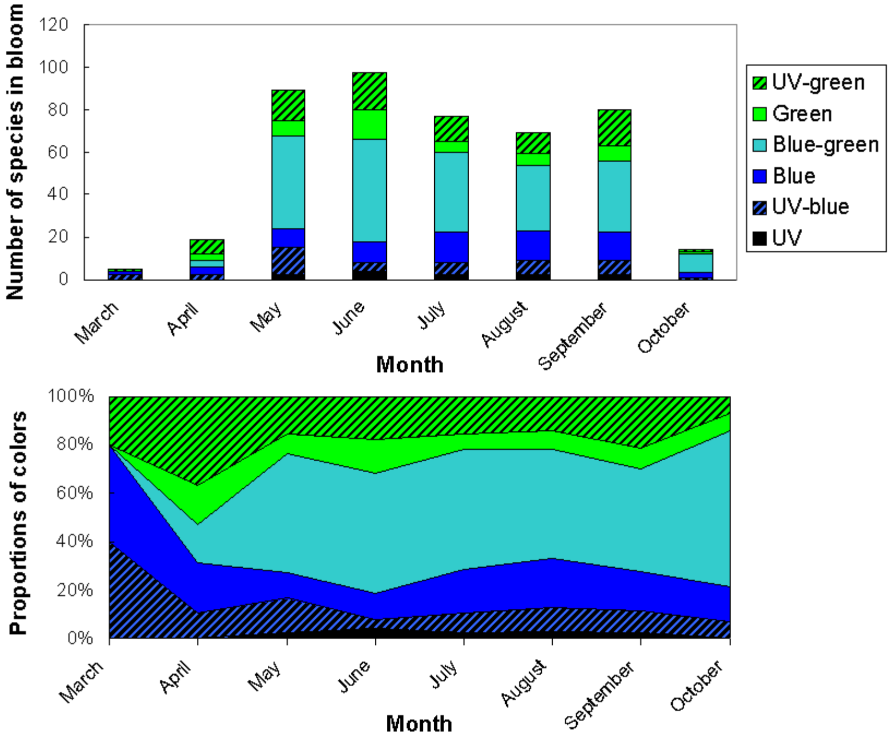

Fig. 3. Bee color distributions for all sites combined. Species are categorized by color as they would appear to a bee. The upper graph shows the absolute counts of species in bloom for all months, while the lower shows the proportions of different colors.

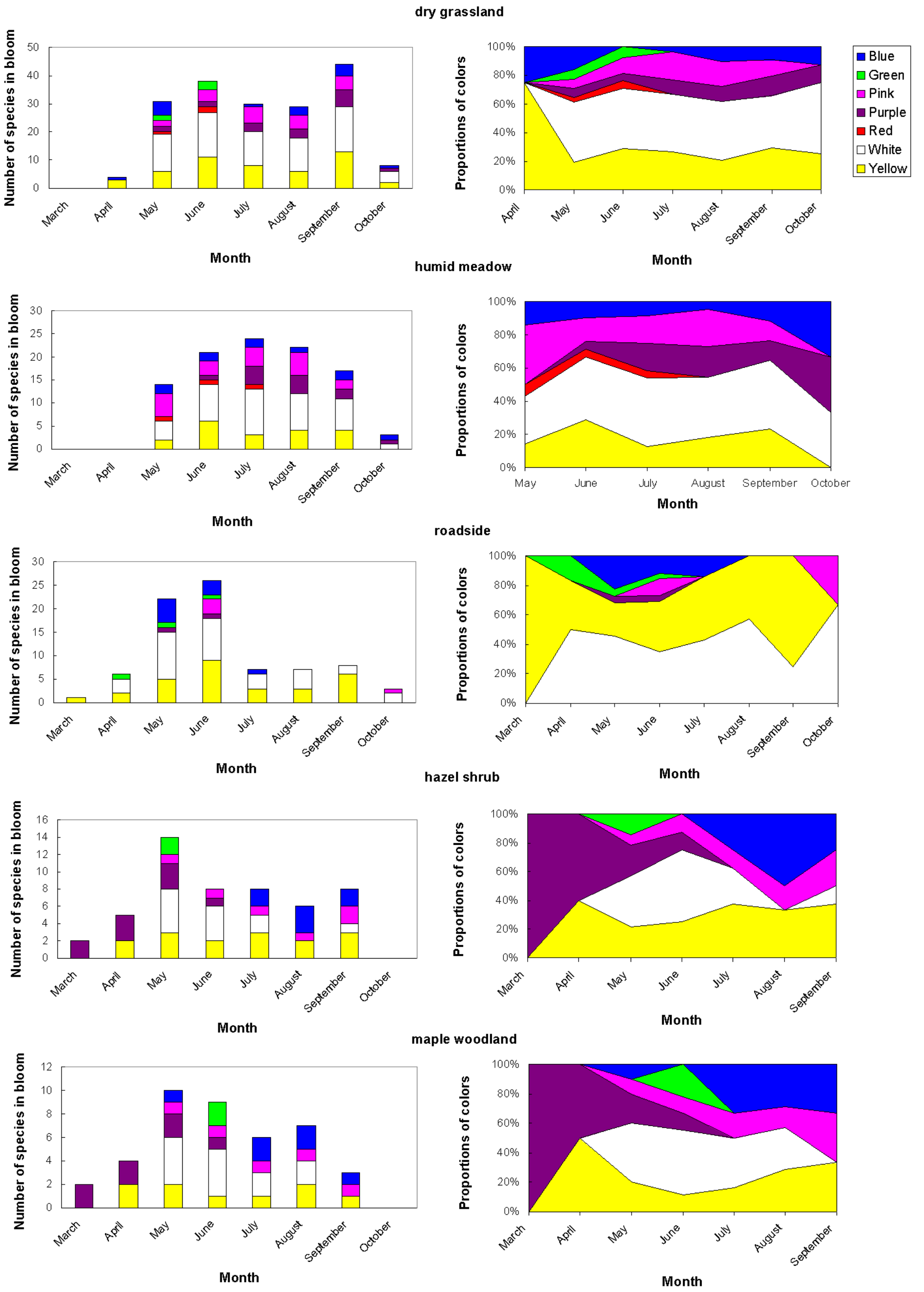

Fig. 4. The proportions of flower colors (as perceived by a human) in the five habitats throughout the year. Left-hand graphs show the absolute counts of flowers in bloom; right-hand graphs show the percentages of the different colors present each month.

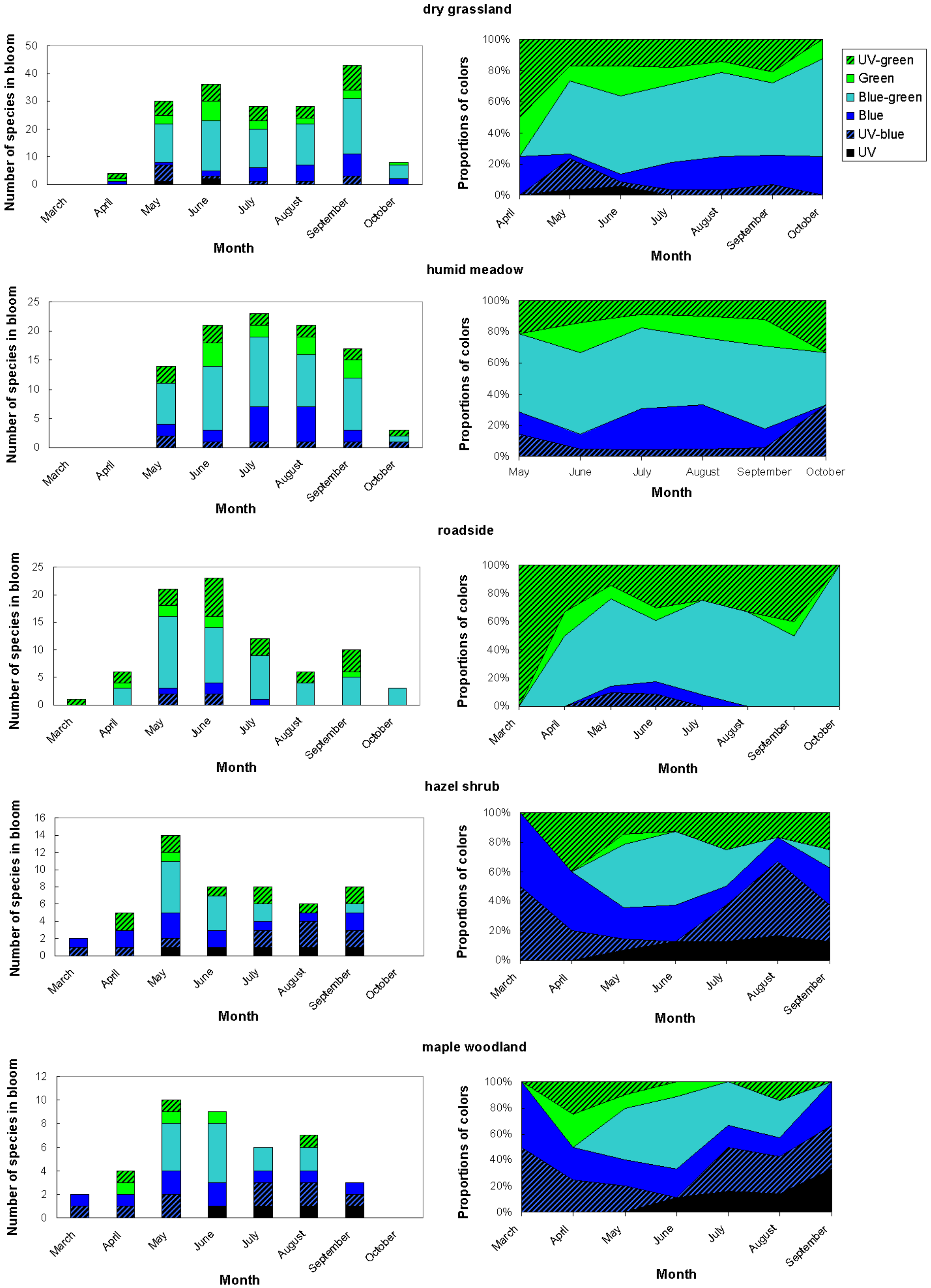

Fig. 5. The proportions of flower colors (as perceived by a bee) in the five habitat types throughout the year. Left-hand graphs show the absolute counts of flowers in bloom; right-hand graphs show the percentages of the different colors present each month.

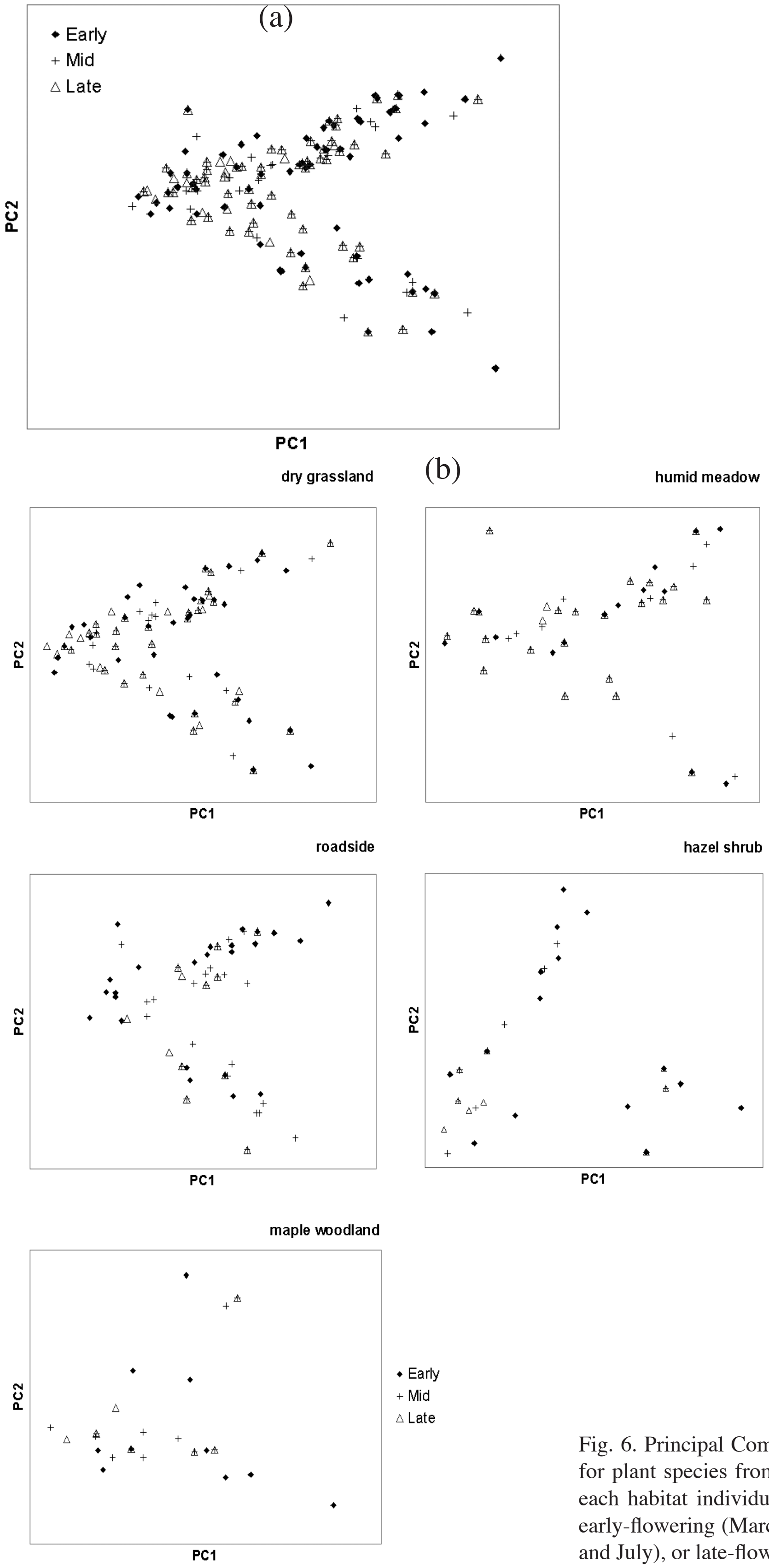

Fig. 6. Principal Components Analysis of reflectance spectra for plant species from (a) all five habitats combined and (b) each habitat individually. Flower species are categorized as early-flowering (March to May), mid-season-flowering (June and July), or late-flowering (August to October).

year, and indeed this is supported by the statistics: early-, mid-, and late-blooming species overall form statistically indistinguishable groups (Hotelling's Trace, $F = 0.028$, $p = 0.166$, $hdf = 4$, $edf = 460$). When each habitat is taken individually, to discover whether any trends are present in a particular habitat that are masked when data from all five locations are pooled, there is also no statistical difference between the spectra of early-, mid-, and late-flowering species (Hotelling's Trace, dry grassland: $F = 0.015$, $p = 0.766$; humid meadow: $F = 0.018$, $p = 0.875$; roadside: $F = 0.061$, $p = 0.416$; hazel shrub: $F = 0.187$, $p = 0.213$; maple woodland: $F = 0.042$, $p = 0.894$).

The comparison of matrices revealed that there was no significant correlation between the spectral properties of flower species and their phenological properties (Mantel test, $p = 0.072$, $N = 146$). The slight trend towards significance, as in the randomization analysis of human flower colors, may perhaps be caused by a small tendency for closely related flowers to both bloom at the same time of year and possess similar colored pigments with comparable spectra; however, this effect is not strong enough to pass the significance threshold and there is no definitive evidence that any slight association can exert an effect in a community containing so many species that are only very distantly related.

DISCUSSION

Previous studies have considered the selective forces that determine when a plant should come into flower (Heinrich, 1976; Kochmer and Handel, 1986; Ollerton and Lack, 1992), and whether more species of flowers possess particular colors at particular times of year (Robertson, 1924; McCann, 1986; Warren and Billington, 2005). The pollination syndrome hypothesis might lead us to expect that if particular pollinator guilds constitute a larger proportion of the total pollinators at certain times of year, then those plant species blooming at that time should be more likely to possess the flower colors associated with those pollinators. In our study, we sought to test this; especially, we attempted to probe the previous observations based on colors as perceived by human observers, and the ecological relevance of these, by modelling flower colors as they are seen by the most important pollinator in our study community, the bees, and also by removing the bias of any color vision system and simply considering the flower colors in the form of their reflectance spectra. Unlike some previous studies (e.g., McCann, 1986), we also address these questions by using robust statistical analyses rather than merely subjective judgements of trends.

Consequently, although superficial examination of the data collected appears to suggest that in some habitats, certain colors of flowers bloom at particular times of year, the statistics show that these observations are largely unsupported. We found no statistically significant evidence that the colors of flowers (as perceived by bee pollinators, or considered in terms of physical reflectance) change throughout the year. We did obtain a single significant finding: a trend for plants flowering in certain months to have the same human colors. This could be taken to be consistent with previous observations of particular human colors dominating at different times of year (McCann, 1986; Warren and Billington, 2005). However, even this significant result breaks down if the analysis takes into account the phylogeny of the species in the habitats.

Thus our findings support the hypothesis of Heinrich (1975), that selection will tend to favor a variety of colors of flower at any given time of year in order to attract pollinators. It has been shown that several bee species will readily learn to associate any flower color with a reward (Menzel, 1985b; Chittka et al., 1992) and that many other insect species are similarly capable of associative learning (Kelber, 1996; Kinoshita et al., 1999), and therefore distinctiveness is generally likely to be more of an asset than being any particular color catering to an innate basis. Indeed, the majority of pollinators in the field will have learning experience influencing their flower visitation decisions rather than being guided by innate preferences alone. Distinctiveness and detectability are also beneficial in light of more recent experiments demonstrating that flower constancy only holds over the short term, as a result of insect memory dynamics (Menzel, 2001; Raine and Chittka, 2005, 2007): a foraging bee will not necessarily remain loyal to a color or species of flower indefinitely, and might frequently shift to other species if the previously visited variety is not available in the immediate vicinity. These observations of insect learning and switching behavior are consistent with our results, which demonstrate a broad range of flower colors present in all habitats studied throughout the year rather than periods in which single flower colors dominate.

We also investigated the phenology of flower colors in different types of habitat, looking at three "open" habitats based largely on grassland, and two "woodland" habitats. Different habitats may have different pollinators and present different foraging conditions for those pollinators, and also present the flowers themselves with different challenges. It is already known that in woodland areas, understorey plants flower earlier (Heinrich, 1976) (see left-hand graphs in Figs. 4 and 5), in order to maximize their growth and productivity before the trees come into full leaf and shade them out. The light environment in woodland areas is also distinctive, and this could perhaps impact on pollinators' foraging choices. During much of the year, pollinators in woodland must forage under lower light levels, and also under light that is spectrally different from normal daylight (with a spectral peak around 550 nm owing to filtering through green leaves) (Endler, 1993); it is still unknown how this may affect their foraging strategies and color preferences. For example, some colors of flower may be less salient or harder to discriminate under woodland light than under ordinary daylight, making such colors disadvantageous when the canopy is closed. While it is known that bees at least have good color constancy and are able to recognize colors accurately under a variety of illuminants (Werner et al., 1988; Lotto and Chittka, 2005), it is also known that their color constancy is not perfect (Dyer, 1999, 2006; Dyer and Chittka, 2004). The extent to which switching between light habitats while foraging induces "mistakes" (visits to an "unintended" flower species) as a result of imperfect constancy remains to be determined.

However, our results did not provide any evidence of a shift in the colors of woodland flower species between early spring (minimal leaf cover) and late spring/summer (more intense leaf cover). There was no trend for woodland flowers blooming in particular months to share the same color more often than expected by chance, as one might predict if particular colors dominated at certain times of year and if some colors increased or decreased in importance later in the year. We found no evidence that plant species in these habitats changed in relative frequencies of colors throughout the year, in a way that could be related to the level of leaf coverage. We also found no evidence of shifts in the spectral composition of the woodland plant communities.

Our results show that previous records of flower colors changing over the year can vary depending on the visual system used to classify flower colors. Flower species that are closely related may share both similar flowering times and similar pigmentation, possibly resulting in apparent abundances of particular colors, as perceived by humans, at particular times of year. However, this pattern is not reflected in the trends in flower color as perceived by bees that we observed in our study sample, nor is the trend borne out in analyses of the spectral reflectances of species in our study sites. Thus our findings demonstrate that we should be wary about drawing conclusions about patterns in flower color based on human perception alone.

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APPENDICES

Phenology tables for the five habitats. x indicates that the corresponding species was observed in bloom during that month; no x indicates that the species was not observed to flower during that month.

APPENDIX I

Phenology table for the dry grassland

										Flower color	
Family	Species	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	Humans	Bees
Apiaceae											
	Aegopodium podagria				x					white	blue-green
	Anthriscus silvestris			x	x					white	blue-green
	Pimpinella major					x	x	x		white	blue-green
	Peucedanum oreoselinum				x	x	x			white	blue-green
Asclepidaceae											
	Cynanchum vincetoxicum			x	x		x	x		white	blue-green
Asteraceae											
	Achillea millefolium				x	x	x	x	x	white	blue-green
	Cirsium arvense					x	x	x		pink	blue-green
	Cirsium oleraceum					x	x	x		white	blue-green
	Cirsium palustre					x	x	x		purple	blue
	Conyza canadiensis					x	x	x		white	blue-green
	Eupatorium cannabinum					x	x	x		pink	blue-green
	Hieracium sabaudum							x		yellow	UV-green
	Matricaria maritima				x					white	blue-green
	Mycelis muralis							x		yellow	UV-green
	Senecio vernalis		x	x						yellow	UV-green
	Senecio viscosus							x		yellow	UV-green
	Senecio vulgaris							x	x	yellow	green
	Sonchus arvensis					x	x	x		yellow	UV-green
	Taraxacum officinale		x	x				x		yellow	UV-green
Boraginaceae											
	Lithospernum arvensis			x						white	blue-green
	Myosotis arvensis			x			x	x		blue	blue-green
	Myosotis hispida			x						blue	blue
Brassicaceae											
	Alliaria petiolata			x	x		x	x		white	blue-green
	Arabis glabra			x	x	x				white	blue-green
	Berteroa incana					x	x	x	x	white	blue-green
	Capsella bursa-pastoris			x	x			x		white	blue-green
	Erysimum cheiranthoides					x				yellow	UV-green
Campanulaceae											
	Campanula rotundifolia							x		blue	blue
	Campanula trachelium					x	x	x		blue	UV-blue
Caprifoliaceae											
	Viburnum opulus			x						white	blue-green
Caryophyllaceae											
	Arenaria serpyllifolia			x						white	blue-green
	Cerastium arvense			x						white	blue-green
	Dianthus carthusianum				x	x	x	x	x	purple	blue
	Holosteum umbellatum			x						white	blue-green
	Melandrium album				x	x	x	x		white	blue-green
	Myosoton aquaticon									white	blue-green
Convolvulaceae											
	Calystegia sepium				x	x	x	x		white	blue-green

APPENDIX I *continued*

										Flower color	
Family	Species	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	Humans	Bees
Cornaceae											
	Cornus sanguinea				x			x		white	blue-green
Crassulaceae											
	Sedum maximum					x		x	x	white	blue-green
	Sedum sexangulare				x	x	x			yellow	green
Euphorbiaceae											
	Euphorbia cyparissias			x	x					green	green
Fabaceae											
	Astragalus glycyphyllos				x					green	blue-green
	Coronilla varia				x					pink	blue-green
	Trifolium campestre				x					yellow	green
	Trifolium dubium				x					yellow	green
	Vicia sativa			x						purple	UV-blue
	Vicia sepium			x						blue	UV-blue
Geraniaceae											
	Geranium robertianum			x	x	x	x	x		pink	blue
Guttiferae											
	Hypericum perforatum				x	x	x	x		yellow	UV-green
Lamiaceae											
	Clinopodium vulgare							x		purple	blue
	Galeopsis pubescens						x	x		pink	blue
	Galeopsis tetrahit				x					pink	blue-green
	Glechoma hederacea									purple	blue
	Salvia pratensis			x	x			x		purple	UV-blue
	Stachys rectus			x	x			x	x	white	blue-green
Liliaceae											
	Allium oleraceum					x				pink	blue
	Asparagus officinalis			x	x					green	green
	Gagea pratensis		x							yellow	UV-green
	Polygonatum odoratum			x						white	blue-green
Onagraceae											
	Epilobium angustifolium				x	x	x	x		pink	blue
	Epilobium hirsutum					x	x	x		purple	blue
Papaveraceae											
	Chelidonium majus			x	x	x	x	x		yellow	UV-green
	Papaver dubium				x					red	UV
	Papaver rhoeas			x	x					red	UV
	Papaver somniferum									red	UV
Primulaceae											
	Primula veris		x	x						yellow	green
Ranunculaceae											
	Ranunculus acris				x					yellow	UV-green
	Thalictrum minus				x	x		x		yellow	green
Rosaceae											
	Fragaria viridis			x						white	blue-green
	Geum rivale			x						pink	UV-blue
	Geum urbanum			x	x	x	x	x		yellow	UV-green
	Potentilla argentea				x			x		yellow	UV-green
	Potentilla heptaphylla			x						yellow	UV-green
	Rosa canina				x					pink	blue-green
	Rubus caesius				x	x	x	x		white	blue-green
Rubiaceae											
	Galium aparine			x	x	x	x			white	blue-green

APPENDIX I *continued*

										Flower color	
Family	Species	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	Humans	Bees
	Galium mollugo				x					white	blue-green
	Galium verum				x	x	x	x		yellow	green
Scrophulariaceae											
	Linaria vulgaris							x	x	yellow	blue-green
	Veronica arvensis		x							blue	blue
	Veronica chamaedrys				x					blue	UV-blue
	Veronica spicata						x	x	x	blue	blue
	Veronica prostrata			x						blue	UV-blue
Solanaceae											
	Solanum dulcamara							x		purple	UV-blue
	Solanum nigrum							x		white	blue-green

APPENDIX II

Phenology table for the humid meadow

										Flower color	
Family	Species	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	Humans	Bees
Apiaceae											
	Aegopodium podagrarium				x					white	blue-green
	Anthriscus silvestris			x	x					white	blue-green
	Peucedanum oreoselinum					x	x	x		white	blue-green
	Pimpinella major					x	x			white	blue-green
	Torilis japonica					x	x			white	blue-green
Asteraceae											
	Achillea millefolium					x		x		white	blue-green
	Bellis perennis			x						white	blue-green
	Chamomilla recutita				x					white	blue-green
	Cirsium oleraceum					x	x	x	x	white	blue-green
	Crepis paludosa				x					yellow	UV-green
Boraginaceae											
	Myosotis arvensis				x	x		x		blue	blue-green
	Symphytum officinale					x				purple	blue
Brassicaceae											
	Cardamine pratensis			x						pink	blue-green
Campanulaceae											
	Campanula patula				x	x	x	x	x	purple	UV-green
Caryophyllaceae											
	Cerastium arvense			x	x					white	blue-green
	Cerastium holosteoides			x	x	x	x			white	blue-green
	Lychnis flos-cuculi			x	x	x	x			pink	blue
	Stellaria palustris				x					white	blue-green
Fabaceae											
	Lathyrus pratensis				x	x	x	x		yellow	green
	Lotus corniculatus				x	x	x	x		yellow	green
	Trifolium campestre				x		x	x		yellow	green
	Trifolium pratense			x	x	x	x	x		pink	blue
	Trifolium repens				x	x	x	x		white	blue-green
	Vicia cracca					x	x			purple	blue
Lamiaceae											
	Ajuga genevensis			x						blue	UV-blue
	Mentha aquatica						x	x		pink	blue-green
	Mentha arvensis						x			pink	blue
	Prunella vulgaris					x	x			blue	blue

APPENDIX II *continued*

Family	Species	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	Flower color	
										Humans	Bees
Liliaceae											
	Allium oleraceum					x				pink	blue
Lythraceaex											
	Lythrum salicaria					x	x			purple	UV-blue
Onagraceae											
	Epilobium hirsutum						x	x		purple	blue
	Epilobium parviflora					x	x			pink	blue
Polygonaceae											
	Polygonum bistorta			x	x					pink	blue-green
	Rumex acetosa			x	x	x				red	blue-green
Ranunculaceae											
	Ranunculus acris			x	x	x	x	x		yellow	UV-green
	Ranunculus repens				x					yellow	green
Rosaceae											
	Filipendula ulmata					x				white	blue-green
	Geum rivale			x						pink	UV-green
	Geum urbanum			x						yellow	UV-green
Rubiaceae											
	Galium mollugo				x	x	x	x		white	blue-green
Scrophulariaceae											
	Veronica chamaedrys			x	x			x	x	blue	UV-blue
Valerianaceae											
	Valeriana sambucifolia					x	x	x		white	blue-green

APPENDIX III

Phenology table for the roadside

Family	Species	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	Flower color	
										Humans	Bees
Apiaceae											
	Pimpinella major					x				white	blue-green
	Torilis japonica					x				white	blue-green
Asteraceae											
	Achillea millefolium				x	x	x	x	x	white	blue-green
	Crepis paludosa				x					yellow	UV-green
	Hieracium murorum				x					yellow	UV-green
	Hieracium pilosella				x					yellow	UV-green
	Hieracium sabaudum							x		yellow	UV-green
	Mycelis muralis				x					yellow	UV-green
	Senecio jacobea					x	x	x		yellow	UV-green
	Senecio vulgaris							x		yellow	green
	Taraxacum officinale		x	x						yellow	UV-green
	Tussilago farfara	x	x							yellow	UV-green
Boraginaceae											
	Myosotis arvensis			x						blue	blue-green
Brassicaceae											
	Arabidopsis thaliana			x						white	blue-green
	Berteroa incana					x	x	x	x	white	blue-green
	Capsella bursa-pastoris			x						white	blue-green
	Cardaminopsis arenosa		x	x	x	x	x	x		white	blue-green
Campanulaceae											
	Campanula patula				x					purple	UV-blue
	Jasione montana					x				blue	blue
Caprifoliaceae											
	Symphoricarpus albus				x					pink	blue

APPENDIX III *continued*

Family	Species	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	Flower color	
										Humans	Bees
Caryophyllaceae											
	Arenaria serpyllifolia			x						white	blue-green
	Cerastium glomeratum			x						white	blue-green
	Cerastium holosteoides				x					white	blue-green
	Holosteum umbellatum			x						white	blue-green
	Silene nutans			x	x					white	blue-green
	Silene vulgaris					x		x		white	blue-green
	Stellaria graminea				x					white	blue-green
	Stellaria holostea			x	x					white	blue-green
Cornaceae											
	Cornus sanguinea				x					white	blue-green
Dipsacaceae											
	Knautia arvensis					x			x	pink	blue-green
Euphorbiaceae											
	Euphorbia cyparissias		x	x	x					green	green
Fabaceae											
	Lathyrus vernus			x						purple	blue
	Trifolium dubium			x						yellow	green
	Trifolium campestre				x					yellow	green
	Trifolium pratense				x					pink	blue
	Trifolium repens				x					white	blue-green
	Vicia hirsuta			x	x					blue	blue-green
	Vicia sepium			x						blue	UV-blue
Guttiferae											
	Hypericum perforatum				x	x	x	x		yellow	UV-green
Lamiaceae											
	Ajuga genevensis			x	x					blue	UV-blue
Ranunculaceae											
	Ranunculus acris			x	x					yellow	UV-blue
	Ranunculus repens				x					yellow	green
Rosaceae											
	Agrimonia eupatoria					x	x	x		yellow	UV-green
	Fragaria vesca			x	x					white	blue-green
	Geum urbanum				x					yellow	UV-green
	Potentilla argentea			x	x	x		x		yellow	UV-green
	Potentilla reptans			x						yellow	UV-green
	Prunus padus		x	x						white	blue-green
	Prunus spinosa		x	x						white	blue-green
	Rubus caesius				x	x				white	blue-green
Scrophulariaceae											
	Linaria vulgaris						x	x		yellow	blue-green
	Veronica chamaedrys			x	x					blue	UV-blue

APPENDIX IV

Phenology table for the maple forest

Family	Species	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	Flower color	
										Humans	Bees
Apiaceae											
	Aegopodium podagraria				x					white	blue-green
	Anthriscus silvestris			x	x					white	blue-green
	Torilis japonica					x				white	blue-green
Asteraceae											
	Cirsium							x		white	blue-green
Balsaminaceae											
	Impatiens parviflora			x	x	x	x	x		yellow	UV
Boraginaceae											
	Pulmonaria obscura	x	x	x						purple	UV-blue
Brassicaceae											
	Alliaria petiolata			x						white	blue-green
Campanulaceae											
	Campanula latifolia						x	x		blue	UV-blue
	Campanula rapunculoides					x	x	x		blue	UV-blue
	Campanula trachelium					x	x			blue	UV-blue
Caryophyllaceae											
	Arenaria serpyllifolia			x						white	blue-green
Geraniaceae											
	Geranium robertianum			x	x	x	x	x		pink	blue
Lamiaceae											
	Galeopsis pubescens							x		pink	blue
	Stachys sylvatica				x					purple	blue
Liliaceae											
	Maianthemum bifolium			x						white	blue-green
	Paris quadrifolia			x						green	green
	Polygonatum multiflorum			x						green	blue-green
Papaveraceae											
	Chelidonium majus			x		x		x		yellow	UV-green
Ranunculaceae											
	Anemone ranunculoides		x							yellow	UV-green
	Hepatica nobilis	x	x	x						purple	blue
	Ranunculus ficaria		x							yellow	UV-green
	Ranunculus sceleratus			x						yellow	UV-green
Rosaceae											
	Geum urbanum				x	x	x	x		yellow	UV-green
	Rubus caesius				x	x				white	blue-green
Rubiaceae											
	Galium aparine			x	x					white	blue-green
Scrophulariaceae											
	Lathraea squamaria		x	x						pruple	blue

APPENDIX V

Phenology table for the maple forest

										Flower color	
Family	Species	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	Humans	Bees
Apiaceae											
	Aegopodium podagraria				x					white	blue-green
	Anthriscus silvestris			x	x					white	blue-green
	Torilis japonica					x	x			white	blue-green
Balsaminaceae											
	Impatiens parviflora				x	x	x	x		yellow	UV
Boraginaceae											
	Pulmonaria obscura	x	x	x						purple	UV-blue
Brassicaceae											
	Alliaria petiolata			x						white	blue-green
Campanulaceae											
	Campanula latifolia						x	x		blue	UV-blue
	Campanula rapunculoides					x				blue	UV-blue
	Campanula trachelium					x	x			blue	UV-blue
Caryophyllaceae											
	Arenaria serpyllifolia			x						white	blue-green
	Stellaria holostea			x	x					white	blue-green
Geraniaceae											
	Geranium robertianum			x	x	x	x	x		pink	blue
Lamiaceae											
	Galeopsis pubescens									pink	blue
	Stachys sylvatica				x					purple	blue
Liliaceae											
	Paris quadrifolia				x					green	green
Papaveraceae											
	Chelidonium majus			x						yellow	UV-green
Primulaceae											
	Primula veris		x	x						yellow	green
Ranunculaceae											
	Anemone ranunculoides		x							yellow	UV-green
	Hepatica nobilis	x	x	x						purple	blue
Rosaceae											
	Geum urbanum						x			yellow	UV-green
	Rubus caesius					x	x			white	blue-green
Rubiaceae											
	Galium aparine				x					white	blue-green
Scrophulariaceae											
	Scrophularia nodosa				x					green	blue-green
	Veronica chamaedrys			x						blue	UV-blue