



## Native or Exotic? Double or Single? Evaluating Plants for Pollinator-friendly Gardens

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In a series of dawn-to-dusk studies, we examined the nature and accessibility of nectar rewards for pollinating insects by monitoring insect visits and the secretion rate and standing crop of nectar in the British native plant species *Salvia pratensis*, *Stachys palustris*, *S. officinalis*, *Lythrum salicaria*, *Linaria vulgaris*, the non-native *Calendula officinalis*, *Petunia × hybrida*, *Salvia splendens*, and the possibly introduced *Saponaria officinalis*. We also compared single with double variants of *Lotus corniculatus*, *Saponaria officinalis*, *Petunia × hybrida* and *Calendula officinalis*. All the British species studied are nectar-rich and are recommended for pollinator-friendly gardens. They showed maximal secretion rates of about 10–90 µg sugar per flower h<sup>-1</sup>, and most had mean standing crops of about 5–60 µg sugar per flower. In all British species studied, the corolla was deep enough for the relatively long-tongued bumblebee *Bombus pascuorum*, but the shallower flowers of *Lythrum salicaria* were also much visited by shorter-tongued bees and hoverflies, as well as by butterflies. The exotic *Salvia splendens*, presumably coevolved with hummingbirds in the Neotropics, has such deep flowers that British bees cannot reach the nectar except by crawling down the corolla. With a secretion rate approaching 300 µg sugar per flower h<sup>-1</sup> and little depletion by insects, *S. splendens* accumulated high standing crops of nectar. *S. splendens*, and single and double flowers of the two probably moth-pollinated species *Petunia × hybrida* and *Saponaria officinalis*, received few daytime visits despite abundant nectar but *Calendula* was well visited by hoverflies and bees. We compared single and double variants of *Lotus corniculatus*, *Petunia × hybrida* and *Calendula officinalis*, and also *Saponaria officinalis*, the last being probably introduced in Britain (Stace, 1997 *New flora of the British Isles*. 2nd edn. Cambridge: Cambridge University Press). In *Petunia*, *Saponaria* and *Lotus*, double flowers secreted little or no nectar. In *Calendula*, where doubling involved a change in the proportion of disc and ray florets rather than modification of individual flower structure, double and single capitula had similar standing crops of nectar. Except in *Calendula*, exotic or double flowers were little exploited by insect visitors. In the exotics, this was probably due to the absence or scarcity of coevolved pollinators, coupled, in double flowers, with the absence of nectar.

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**Key words:** *Salvia pratensis*, *Salvia splendens*, *Stachys palustris*, *Stachys officinalis*, *Lythrum salicaria*, *Linaria vulgaris*, *Lotus corniculatus*, *Saponaria officinalis*, *Petunia × hybrida*, *Calendula officinalis*, wild flowers, double flowers, gardens, nectar, secretion rate, standing crop, pollinators, bumblebees, *Bombus*, honeybees, *Apis*, hoverflies, butterflies, *Anthidium manicatum*.

### INTRODUCTION

Populations of some pollinating insects are declining in the UK (Williams, 1986; Warren, 1992). Some long-tongued species of bumblebee are locally extinct in parts of Britain (Williams, 1986), leaving few species able to pollinate deep-flowered crops and wild flowers. Gardens can help to sustain flower-visiting insect populations; and plants with deep, nectar-rich flowers may make a particularly valuable contribution to pollinator conservation by sustaining long-tongued butterflies and giving long-tongued bee species a nectar refuge from honeybee competition (Corbet *et al.*,

1995; Corbet, 2000). The British flora includes many ornamental, nectar-rich species that might be grown in gardens. Having evolved in the local pollinator climate, these are expected to offer rewards accessible to British insects. Some British plant species suitable for pollinator-friendly gardens have been considered elsewhere (Comba *et al.*, 1999a). Here we describe a further study in a British garden in which we investigated nectar and insect visits to British species of *Stachys*, *Salvia*, *Lythrum*, *Linaria* and *Lotus*, the naturalized or native *Saponaria*, and exotic species of *Petunia*, *Salvia* and *Calendula*.

Double cultivars have long been grown in gardens (Coats, 1956). With supernumerary petals often replacing anthers and carpels, they are popular for their novel appearance (Reynold and Tampion, 1983). A further possible advantage to gardeners is that in the absence of seed set the flowering season may be extended (Walters, 1993). However, double flowers are suspected of having little value for wildlife. Where doubling reduces or eliminates seed set, less food is supplied for seed-feeding animals. Flower-visiting insects may also be affected. Pollen production will be reduced if

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petals replace anthers, and in some species double flowers secrete little or no nectar (Comba *et al.*, 1999b). We compared double and single variants of *Lotus corniculatus* L., *Petunia* × *hybrida* (Hook.) Vilm., *Calendula officinalis* L. and *Saponaria officinalis* L.

In conjunction with data from our earlier studies (Comba *et al.*, 1999a, b), our findings allow us to identify types of ornamental flower suitable for pollinator-friendly gardens. Throughout this paper nomenclature follows Stace (1997) and Huxley (1992) for plants; Prŷs-Jones and Corbet (1991) for bumblebees, in which the two closely similar species *Bombus terrestris* (L.) and *B. lucorum* (L.) were not separated; Fitton *et al.* (1978) for other bees; and Chandler (1998) for hoverflies.

## MATERIALS AND METHODS

### *The plant species*

Wood betony (*Stachys officinalis* (L.) Trevis.) and marsh woundwort (*Stachys palustris* L.) are widespread in Europe and common in Britain, although *S. officinalis* is rare in East Anglia and Ireland, and both species are scarce in Scotland. Both were valued as medicinal herbs, and *S. officinalis* was often grown in monastery gardens (Hamilton *et al.*, 2000). Our earlier comparison of *S. palustris* with *S. sylvatica* showed both to be nectar rich and visited by long-tongued bees, including the solitary bee *Anthidium manicatum*, whose territorial behaviour contributes to garden interest (Comba *et al.*, 1999a).

Meadow clary (*Salvia pratensis* L.) and scarlet sage (*Salvia splendens* Sell ex Roem. & Schult.) belong to a genus that includes about 900 species, several of which are grown in gardens (Huxley, 1992). Among these are native European species with lilac-purple flowers pollinated by bees, and exotic species from the New World tropics with scarlet flowers pollinated by hummingbirds (Meeuse and Morris, 1984). We compared the lilac-purple *Salvia pratensis*, native but local in Britain, with the exotic *Salvia splendens*, introduced from the Neotropics to Britain in 1822 (Coats, 1956) and commonly grown as a half-hardy annual bedding plant in parks and gardens.

Purple loosestrife (*Lythrum salicaria* L.) is a common wildflower in British wetlands (Huxley, 1992). It is widely grown in British gardens (Huxley, 1992) where the trimorphic flowers, massed in conspicuous spikes, are visited by a wide range of insects including butterflies, bees and hoverflies (Knuth, 1906–1909; Comba *et al.*, 1999a; Corbet, 2000).

Common toadflax (*Linaria vulgaris* Mill.) is common in waste places in most of the British Isles (Stace, 1997). It is one of several species of *Linaria* grown in gardens (Huxley, 1992). An insect requires force to open the personate flowers and the nectar is held in a deep spur. Long-tongued bees can take nectar via the mouth of the flower, and shorter-tongued bees may take nectar through a hole bitten in the corolla (Knuth, 1906–1909; Corbet *et al.*, 1981).

Birdsfoot trefoil (*Lotus corniculatus* L.) is a native British species recommended for inclusion in flowering meadows as a nectar source for bees and butterflies and as a larval

foodplant for butterflies (Huxley, 1992). We compared the single with the double form ('Flore Pleno', 'Plenum').

Soapwort (*Saponaria officinalis* L.), native or more probably naturalized in Britain since at least 1629, has long been grown as an ornamental, a medicinal herb and as a source of saponins for washing. The double form was established in gardens by 1659 (Coats, 1956). Knuth (1906–1909) described the single form of soapwort *Saponaria officinalis* as a hawkmoth flower, and Jürgens *et al.* (1996) drew attention to features characteristic of spingophily: flower-opening at dusk, nocturnal scent, pale colour and a deep corolla. They saw noctuid moths taking nectar legally, *Bombus terrestris/lucorum* robbing, and hoverflies taking pollen, but they did not see hawkmoths visiting *Saponaria*.

*Petunia* (*Petunia* × *hybrida* (Hook.) Vilm.) probably arose from hybrids between *P. axillaris* (Lam.) Britton, Sterns & Poggenb. and *P. integrifolia* (Hook.) Schinz & Thell. It includes two main kinds: Grandiflora hybrids with few large flowers; and Multiflora hybrids with more numerous, smaller flowers (Huxley, 1992). *Petunia* species came from tropical South America to Britain, where these frost-tender perennials are generally grown as annuals, in the early nineteenth century. The pollinators of the ancestral *Petunia* species in South America are unknown. Darwin (1876) studied *P. integrifolia* (as *P. violacea*) and commented on the rarity of insect visits to its flowers by day. In his garden, flowers protected from insect visits yielded little or no seed, whereas exposed flowers yielded abundant seed, indicating that some insect pollinators were present. He regarded moths as the likely pollinators, and cited reports of moths, especially hawkmoths, visiting the flowers in Germany and England. The pale colour and nocturnal scent of the ancestral *P. axillaris* (Huxley, 1992) are compatible with moths as coevolved pollinators.

Pot marigold (*Calendula officinalis* L.) probably reached Britain by the thirteenth century (Coats, 1956). It has long found culinary and medicinal uses, and is grown as an ornamental and recommended as an attractant for natural enemies of pests in the vegetable garden, particularly for hoverflies whose larvae eat aphids (Pears and Strickland, 1995). We compared the single form with the nominally double cultivar 'Orange King'.

Plants were grown in the Cambridge University Botanic Garden, UK, and flowered in June and July 1998 and 1999. Generally, each species occupied a plot 5 m long × 1 or 1.5 m wide. Variants to be compared were in adjacent plots, but the two species of *Salvia* were in a row of alternating 1 m<sup>2</sup> plots, the two variants of *Lotus corniculatus* occupied adjacent 3 × 1 m plots, and the single flowered *Saponaria* was in a 7.2 × 2 m plot adjacent to seven plants of the double form.

Floral measurements were made using digital callipers (Mitutoyo (UK) Ltd, Andover, UK). The detached head of the longest-tongued bumblebee species present, *Bombus hortorum* (L.), was mounted on a pin with its tongue extended, and used as a probe to see which parts of *Petunia* flowers were within its reach. Flower movements in *Calendula* were monitored by measuring the overall diameter of ten capitula at regular intervals for 2 d. Numbers of open flowers were estimated from counts in

1 m<sup>2</sup> quadrats or, where practicable, flowers were counted directly.

Rates of nectar secretion and depletion change with weather and time of day so that evaluation of reward production and insect exploitation demands regular sampling throughout the day, preferably on more than 1 d (Comba, 1999a, b). Accordingly we sampled nectar, microclimate and insect visits at regular intervals from dawn to dusk. We sampled *Stachys palustris* and *Stachys officinalis* on 7 and 9 July 1999, *Salvia splendens* and *S. pratensis* on 20 July 1998 and 16 and 19 July 1999, *Lythrum salicaria* on 10 July 1998, *Linaria vulgaris* on 29 June 1998, *Lotus corniculatus* on 15 and 23 July 1998, *Saponaria officinalis* on 23 July 1998, *Petunia × hybrida* on 18 and 30 June 1999, and *Calendula officinalis* on 7 July 1999.

At regular intervals throughout the day, nectar was sampled from open (but not yet senescing) flowers of each species or variant. We tried to withdraw all the nectar from each flower into a glass microcapillary (microcaps; Drummond Scientific Co., Broomall, Pa., USA) holding a standard volume of 0.5, 1 or 5 microlitres; nectar volume was then calculated from the length of the fluid column. Solute concentration (as g sucrose/100 g solution) was measured at once with a pocket refractometer modified for small volumes by the makers (Bellingham & Stanley Ltd, Tunbridge Wells, UK). Nectar sugar content per flower (*s*, µg) was calculated from the equation  $s = 10dvC$ , where *v* is the volume calculated as above (µl), and *d* is the density of a sucrose solution at a concentration *C* (g sucrose/100 g solution) as read on the refractometer (Bolten et al., 1979; Prÿs-Jones and Corbet, 1991). The density was obtained as

$$d = 0.0037921C + 0.0000178C^2 + 0.9988603$$

(Prÿs-Jones and Corbet, 1991).

Samples from different flowers were analysed separately except that in *Calendula* the standing crop in each capitulum was measured by probing all open disc florets on that capitulum with 0.5 µl microcaps and measuring the volume and solute concentration of the pooled sample.

At each sampling time we sampled ten flowers to measure standing crop (the amount of nectar in the flower at a given time, expressed as µg sugar per flower), taking care to avoid damage to the nectaries, and then enclosed these emptied flowers in netting (2 mm mesh or finer) to prevent insect visits for a period, usually of about 2 h, selected after preliminary measurements of secretion rate. These flowers were then resampled for a measure of secretion rate, expressed as µg sugar per flower h<sup>-1</sup>, and tagged so that they would not be sampled again. In *Calendula*, secretion rate was measured in the single variant only, by bagging the capitula whose disc florets had just been emptied for standing crop measurement, and then resampling all open disc florets after about 2 h. The double variant had so many rings of open disc florets that such resampling would have been unreliable.

Temperature affects nectar secretion rate (Búrquez and Corbet, 1998) and insect flight activity (Corbet et al., 1993), so microclimate and insect visits to the flowers were monitored at each sampling time throughout each

dawn-to-dusk study. Microclimate was measured at flower height. Air temperature was measured with a fine thermocouple, and to integrate air temperature with incident radiation, an important determinant of insect body temperature, we also measured black globe temperature, *T<sub>g</sub>*. This was measured in full sunlight as the temperature of a K-type thermocouple inserted in the centre of an 8-mm-diameter sphere of Blu-Tack (Bostik Ltd, Leicester, UK) painted matt black (Joy Black Board Black, Matt Finish, Turnbridges Ltd, London, UK) (Corbet et al., 1993).

At each sampling time, insects foraging on the plot were monitored by recording insects initially present plus all new visitors to the plot during a standard observation period, usually 5 min. In the *Petunia* study, an observer walked slowly around each plot for 3 min, and then watched each plot for 10 min, recording each insect when first seen visiting flowers in the plot. During the dawn-to-dusk study on 15 July 1998, the plots of *Lotus* were monitored continuously throughout the day, and any insect that foraged on the flowers was recorded on entry (or re-entry) to the plot. We recorded the species of insects foraging on the flowers, whether each was taking pollen, nectar or both, and whether it was visiting legally via the mouth of the corolla, or robbing by taking nectar through a hole bitten in the corolla.

## RESULTS

### *Stachys palustris* and *S. officinalis*

Standing crops of nectar in *Stachys palustris*, at up to about 110 µg nectar sugar per flower, were similar to those found earlier in the same species (Comba, 1999a), but secretion rates, at up to about 20 µg sugar per flower h<sup>-1</sup>, were a little higher (Fig. 1). *Stachys officinalis* yielded standing crops and secretion rates similar to those of *S. palustris* (Fig. 1). Both species received substantial numbers of insect visits. With a corolla length of 8.6 ± 0.1 mm (mean ± s.e., *n* = 10), *S. palustris* received most of its visits from bumblebees (mostly *Bombus pascuorum*) and the solitary bee *Anthidium manicatum* (L.), both mostly taking nectar; smaller numbers of visits were made by hoverflies and short-tongued solitary bees of the genus *Lasioglossum*, both mostly taking pollen (Table 1). With a longer corolla (11.5 ± 0.2 mm, *n* = 10), *S. officinalis* received visits from a similar spectrum of insects, mainly bumblebees (again mostly *B. pascuorum*) and *A. manicatum*, both mostly taking nectar, with smaller numbers of visits from hoverflies and *Lasioglossum*, all taking pollen (Table 1). *Bombus terrestris/lucorum* sometimes robbed nectar from *S. officinalis* through a hole bitten in the corolla (Table 1).

### *Salvia pratensis* and *S. splendens*

Dawn-to-dusk studies on both species of *Salvia* (Fig. 2) showed that the two species differed greatly in the secretion rate and standing crop of nectar. The native *S. pratensis* showed secretion rates up to 40–60 µg sugar per flower h<sup>-1</sup>, comparable to those of *Stachys* (see above) (Table 2). With

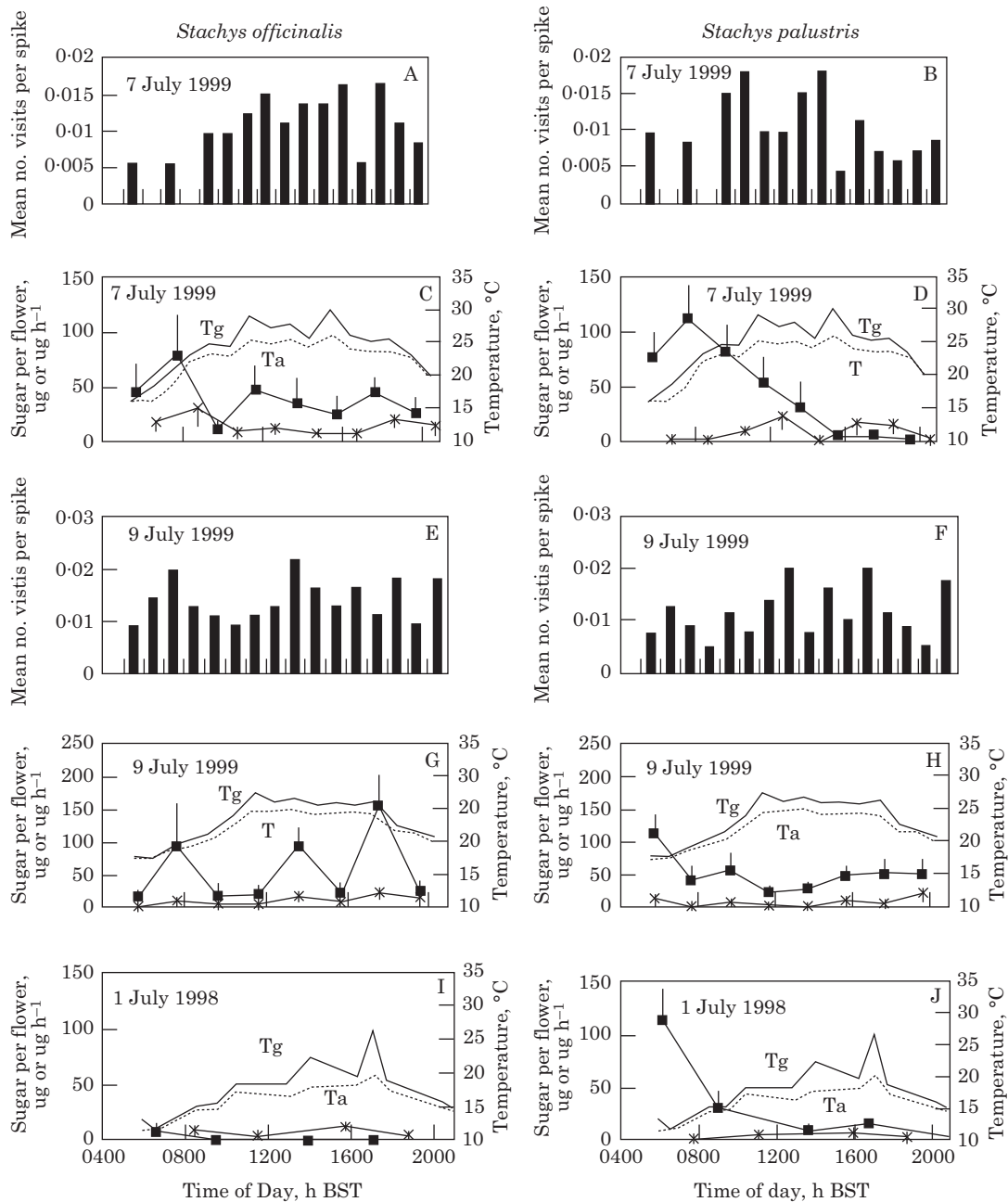


FIG. 1. Results of dawn-to-dusk studies comparing *Stachys officinalis* (A, C, E, G, I) with *S. palustris* (B, D, F, H, J) with respect to nectar secretion rate and standing crop and insect visits on 7 Jul. 1999 (A–D), 9 Jul. 1999 (E–H) and 1 Jul. 1998 (I, J). Insect visitors present or arriving per spike in 5 min are shown in A, B, E and F. Mean (and s.e.) nectar secretion rates (x,  $\mu\text{g}$  sugar per flower  $\text{h}^{-1}$ ) and standing crops (■,  $\mu\text{g}$  sugar per flower) are shown, with ambient (dotted line, Ta) and black globe (continuous line, Tg) temperatures, C, D, G–J. All plots share the same scale on the x-axis.

a corolla length of  $7.6 \pm 0.2$  mm ( $n = 20$ ), its flowers were visited by numerous insects, particularly bees [the bumblebees *Bombus pascuorum* Scopoli, with smaller numbers of *B. hortorum* (L.) and *B. lapidarius* (L.), and some honeybees *Apis mellifera* (L.)] taking nectar, and hoverflies mostly taking pollen (Table 1). Perhaps as a result of so many insect visits, standing crops of nectar were relatively low except early in the morning.

The exotic *S. splendens* had high mean rates of nectar secretion, up to nearly  $300 \mu\text{g}$  sugar per flower  $\text{h}^{-1}$ , and standing crops of nectar sugar of up to about  $1300 \mu\text{g}$  sugar per flower accumulated in the flowers (Table 2). The corolla is  $26.6 \pm 1.2$  mm long ( $n = 20$ ), beyond the reach of the tongue of any British bee. The few visits recorded during our dawn-to-dusk studies involved only pollen collection, by bees and hoverflies (Table 1). On other occasions

TABLE 1. Summed counts through the day (with percentage of visits that took nectar) of insect visitors to flowers of *Salvia* and *Stachys* species during dawn-to-dusk studies on 16 and 19 Jul. (*Salvia*) and 7 and 9 Jul. (*Stachys*) 1999

	<i>Salvia pratensis</i>		<i>Salvia splendens</i>		<i>Stachys palustris</i>		<i>Stachys officinalis</i>	
	16 July	19 July	16 July	19 July	7 July	9 July	7 July	9 July
Spikes m <sup>-2</sup>	89	54	146	129	147	163	145	111
Flowers per spike (mean ± s.e.) (n = 20)	8.6 ± 0.57	7.5 ± 0.85	2.2 ± 0.25	2.5 ± 0.21	11 ± 0.89	13 ± 1.21	18 ± 1.36	15 ± 0.12
<i>Bombus pascuorum</i>	58 (100)	51 (100)	1 (0)	0	23 (96)	34 (100)	27 (100)	34 (100)
Other <i>Bombus</i> spp.	2 (100)	4 (100)	0	0	2 (100)	18 (100)	14 (100)	18 (100)
<i>Apis mellifera</i>	6 (100)	23 (100)	4 (0)	0	0	0	0	0
<i>Anthidium manicatum</i>	0	0	0	0	47 (100)	49 (100)	34 (100)	42 (100)
<i>Lasioglossum</i> spp.	7 (14)	5 (20)	3 (0)	4 (0)	11 (9)	22 (5)	2 (0)	2 (0)
Hoverflies	19 (5)	25 (4)	2 (0)	4 (0)	19 (11)	25 (0)	25 (0)	21 (0)
<i>B. terrestris</i> robbers (included above)	0	0	0	0	0	0	2	8
Total visitors	92 (73)	109 (72)	10 (0)	8 (0)	106 (73)	146 (66)	112 (74)	123 (81)

The last row includes minor species not listed above.

honeybees sometimes crawled right into the corolla, presumably taking nectar.

#### *Lythrum salicaria*

As in our earlier study (Comba *et al.*, 1999a), our dawn-to-dusk study on 10 July 1998 showed a secretion rate of up to nearly 80 µg sugar per flower h<sup>-1</sup> (Fig. 3B, Table 2), frequent insect visits (Fig. 3A) giving a high depletion rate, and a low mean standing crop of up to about 20 µg sugar per flower. With a mean of 28 ± 6 fully-open flowers per flowering spike, and 373 spikes (on 73 plants) in the 5 m<sup>2</sup> plot, the secretion rate was the equivalent of up to 167 mg m<sup>-2</sup> h<sup>-1</sup>.

Foraging insects were monitored for 5 min periods in a 1 m<sup>2</sup> patch containing 92 flowering spikes (2622 flowers) (Fig. 3A). Up to 14 honeybees worked the patch, visiting up to 146 individual flowers in a 5 min period, equivalent to 1.58 visits per spike per 5 min. Up to seven hoverflies at a time visited up to 12 flowers in a 5 min period. *Bombus terrestris/lucorum* made a total of four visits. During insect surveys on 23 July 1998 and 6 and 10 July 1999, honeybees, hoverflies and *B. terrestris/lucorum* visited, with *B. lapidarius* and *B. pascuorum* in addition, as in our earlier study (Comba *et al.*, 1999a). On these occasions there were few butterflies in the area; in an earlier study in the same locality, seven species of butterfly visited *L. salicaria* (Comba *et al.*, 1999a).

#### *Linaria vulgaris*

In a dawn-to-dusk study we found mean standing crops of up to about 570 µg nectar sugar per flower, and a mean secretion rate of up to about 90 µg sugar per flower h<sup>-1</sup> (Fig. 3C, Table 2). The accumulation of such large standing crops implies low rates of depletion. With a mean corolla length (from the mouth to the end of the spur) of 24.9 ± 0.9 mm (n = 10), the flowers were visited by *Bombus terrestris/lucorum*, *B. pascuorum*, *Apis mellifera* and hoverflies, the bees pushing their heads part way into the flowers. The tongue of *A. mellifera* is shorter than the spur of

*L. vulgaris*, and if this species took nectar it must have done so only from flowers in which accumulated nectar had risen up the spur. Elsewhere we have seen *B. hortorum* (L.) probing for nectar legally, through the mouth of the flower, and *B. terrestris* robbing through a hole in the corolla (Corbet *et al.*, 1981).

#### *Lotus corniculatus*

The corolla depth of single flowers, measured between the bend in the top petal and the point at which the calyx narrows, was 6.6 ± 0.04 mm (n = 59). In the double form the corolla was effectively open to the base. Flowers of the double form ('Flore Pleno', 'Plenum') have supernumerary petals and no anthers or carpels (Fig. 4D, F). The double variant of *L. corniculatus* set no seed. Fully-open flowers were tagged on 24 July and examined for fruit set on 3 August 1998. Two hundred and eighty-seven single flowers had formed 138 seed pods 10–36 mm long, but 25 double flowers had formed no pods.

Dawn-to-dusk studies of the single variant showed standing crops of up to about 10–15 µg sugar per flower, especially in the early morning, and secretion rates of up to 10 µg per flower h<sup>-1</sup> (Fig. 5, Table 2). The double variant yielded no nectar, even when ten flowers were sampled after being bagged for 9.5 h to exclude insects. Staining with neutral red (Kearns and Inouye, 1993) showed no sign of nectaries, although similar staining of single flowers showed clusters of red, supposedly nectariferous patches on the wing petals. There were no such patches on the corresponding petals of double flowers, but some other petals showed diffuse red smears.

The 33 plants of the single variant, with 760 flowers on 15 July and over 200 on 23 July, received visits from bees (mostly *Bombus pascuorum*, with *Bombus lapidarius* and *Megachile willughbiella*) and hoverflies. On the 22 plants of the double variant, with 80 flowers on 15 July and 27 on 23 July, no insect visitors were seen during the dawn-to-dusk study on 15 July or over 4 weeks of fieldwork near the plot.

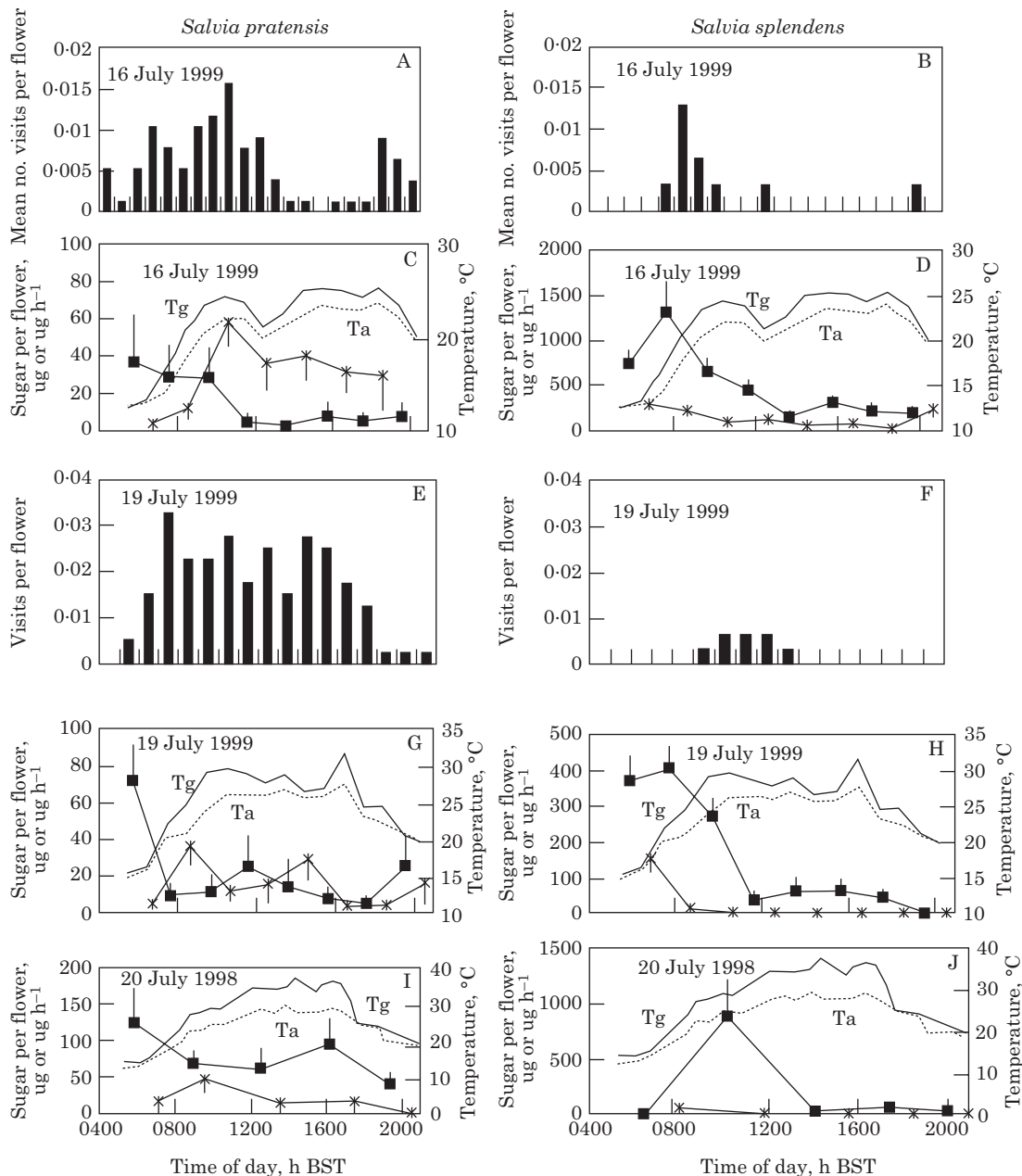


FIG. 2. Results of dawn-to-dusk studies comparing nectar production and insect visits in the native *Salvia pratensis* (A, C, E, G, I) and the exotic *Salvia splendens* (B, C, F, H, J) on 16 Jul. 1999 (A–D), 19 Jul. 1999 (E–H) and 20 Jul. 1998 (I, J). Insect visitors present or arriving per flower in 5 min periods are shown in A, B, E and F. Mean (and s.e.) nectar secretion rates (x,  $\mu\text{g}$  sugar per flower  $\text{h}^{-1}$ ) and standing crops (■,  $\mu\text{g}$  sugar per flower) are shown, with ambient (dotted line, Ta) and black globe (continuous line, Tg) temperatures, in C, D, G–J. Note different vertical scales for sugar per flower in the two species. All plots share the same scale on the x-axis.

### *Saponaria officinalis*

Single flowers contained very high standing crops of nectar, with 1000–2000  $\mu\text{g}$  sugar per flower (Table 2), despite a relatively low secretion rate (Fig. 5D; note different y-axis). Double flowers yielded little or no nectar. In 30 double flowers sampled throughout the day on 23 July 1998, the standing crop was less than 1  $\mu\text{g}$  sugar per flower in all but three (with a surprisingly high maximum of 244  $\mu\text{g}$  per flower), and the secretion rate over periods of

2.5–5 h was too small to measure in 27 of the 30 flowers, and never more than 3  $\mu\text{g}$  per flower  $\text{h}^{-1}$ .

The long-clawed petals of single soapwort emerge from a calyx  $16.8 \pm 0.2$  mm long ( $n = 20$ ), too deep for the nectar to be legally accessible to honeybees or any bumblebees present, except large individuals of the long-tongued *Bombus hortorum* (Fig. 4G, I). The distance from the plane of the petals to the corolla base is  $22.1 \pm 0.1$  mm ( $n = 30$ ). The double form has supernumerary petals and a calyx effectively open to the base, making any nectar

TABLE 2. Summary of nectar measurements from dawn-to-dusk studies

Species	Variant	Date	Standing crop, $\mu\text{g}$ per flower			Secretion rate, $\mu\text{g}$ per flower $\text{h}^{-1}$			Sampling period (h BST)	<i>n</i>
			Maximum $\pm$ s.e.	Minimum $\pm$ s.e.	Mean $\pm$ s.e.	Maximum $\pm$ s.e.	Minimum $\pm$ s.e.	Mean $\pm$ s.e.		
<i>Stachys officinalis</i>	Native	7 Jul. 1999	78 $\pm$ 37	11 $\pm$ 7	38 $\pm$ 7	30 $\pm$ 18	6 $\pm$ 4	14 $\pm$ 3	0540–1942	8
<i>Stachys officinalis</i>	Native	9 Jul. 1999	153 $\pm$ 47	17 $\pm$ 10	55 $\pm$ 18	22 $\pm$ 11	3 $\pm$ 1	10 $\pm$ 2	0542–1937	8
<i>Stachys palustris</i>	Native	7 Jul. 1999	111 $\pm$ 32	2 $\pm$ 1	45 $\pm$ 15	22 $\pm$ 11	0.3 $\pm$ 0.3	8 $\pm$ 3	0542–1937	8
<i>Stachys palustris</i>	Native	9 Jul. 1999	112 $\pm$ 29	23 $\pm$ 9	51 $\pm$ 10	20 $\pm$ 16	0	7 $\pm$ 3	0544–1940	8
<i>Salvia pratensis</i>	Native	16 Jul. 1999	37 $\pm$ 25	3 $\pm$ 3	15 $\pm$ 5	58 $\pm$ 13	4 $\pm$ 3	31 $\pm$ 6	0545–1938	8
<i>Salvia pratensis</i>	Native	19 Jul. 1999	72 $\pm$ 19	6 $\pm$ 4	22 $\pm$ 8	36 $\pm$ 9	5 $\pm$ 3	16 $\pm$ 4	0542–1937	8
<i>Salvia splendens</i>	Exotic	16 Jul. 1999	1318 $\pm$ 339	156 $\pm$ 39	505 $\pm$ 139	291 $\pm$ 59	23 $\pm$ 12	143 $\pm$ 35	0552–1939	8
<i>Salvia splendens</i>	Exotic	19 Jul. 1999	406 $\pm$ 64	0	157 $\pm$ 58	154 $\pm$ 43	0	22 $\pm$ 19	0550–1937	8
<i>Lythrum salicaria</i>	Native	19 Jul. 1998	19 $\pm$ 12	0	5 $\pm$ 3	77 $\pm$ 23	1 $\pm$ 1	29 $\pm$ 12	0652–2042	6
<i>Linaria vulgaris</i>	Native	29 Jun. 1998	566 $\pm$ 150	120 $\pm$ 61	290 $\pm$ 62	88 $\pm$ 15	8 $\pm$ 8	46 $\pm$ 13	0610–2025	5,6
<i>Lotus corniculatus</i>	Single	15 Jul. 1998	12 $\pm$ 6	0	3 $\pm$ 2	10 $\pm$ 2	0	6 $\pm$ 2	0550–1740	6
<i>Lotus corniculatus</i>	Double	15 Jul. 1998	0	0	0	0	0	0	0607–1826	3
<i>Lotus corniculatus</i>	Single	23 Jul. 1998	13 $\pm$ 6	0	5 $\pm$ 2	10 $\pm$ 3	4 $\pm$ 1	6 $\pm$ 1	0614–1915	6
<i>Saponaria officinalis</i>	Single	23 Jul. 1998	1830 $\pm$ 181	1476 $\pm$ 252	1660 $\pm$ 75	50 $\pm$ 16	5 $\pm$ 3	27 $\pm$ 4	0615–1934	4
<i>Saponaria officinalis</i>	Double	23 Jul. 1998	38 $\pm$ 27	0	13 $\pm$ 12	0.5 $\pm$ 0.3	0	0.2 $\pm$ 0.2	0800–1830	3
<i>Petunia</i> $\times$ <i>hybrida</i>	Grandiflora single	18 Jun. 1999	241 $\pm$ 59	125 $\pm$ 32	197 $\pm$ 17	174 $\pm$ 47	12 $\pm$ 8	61 $\pm$ 29	0613–2012	7,5
<i>Petunia</i> $\times$ <i>hybrida</i>	Grandiflora single	30 Jun. 1999	104 $\pm$ 33	45 $\pm$ 27	62 $\pm$ 9	16 $\pm$ 8	4 $\pm$ 3	10 $\pm$ 2	0654–1944	6,5
<i>Petunia</i> $\times$ <i>hybrida</i>	Multiflora single	18 Jun. 1999	472 $\pm$ 65	160 $\pm$ 30	259 $\pm$ 39	378 $\pm$ 60	36 $\pm$ 18	132 $\pm$ 63	0614–2011	7,5
<i>Petunia</i> $\times$ <i>hybrida</i>	Multiflora single	30 Jun. 1999	294 $\pm$ 72	102 $\pm$ 38	157 $\pm$ 29	34 $\pm$ 14	16 $\pm$ 4	23 $\pm$ 3	0651–1944	6,5
<i>Petunia</i> $\times$ <i>hybrida</i>	Multiflora double	Various dates	0	0	0	0	0	0		
<i>Calendula officinalis</i>	Single	7 Jul. 1999	34 $\pm$ 11	3 $\pm$ 1	25 $\pm$ 8	44 $\pm$ 14	0	16 $\pm$ 14	0822–1655	3,4
<i>Calendula officinalis</i>	Double	7 Jul. 1999	50 $\pm$ 28	1 $\pm$ 1	27 $\pm$ 9				0822–1817	5

For standing crop and secretion rate, we give the mean ( $\pm$ s.e.) of the *n* means for the *n* sampling times during the day, and the maximum and minimum mean (with s.e.) for any sampling time during the day. Standing crops for *Calendula* are given as  $\mu\text{g}$  sugar per capitulum, but all other values are in  $\mu\text{g}$  sugar per flower. The sampling period is given because it may influence the maximum, minimum and mean nectar values.

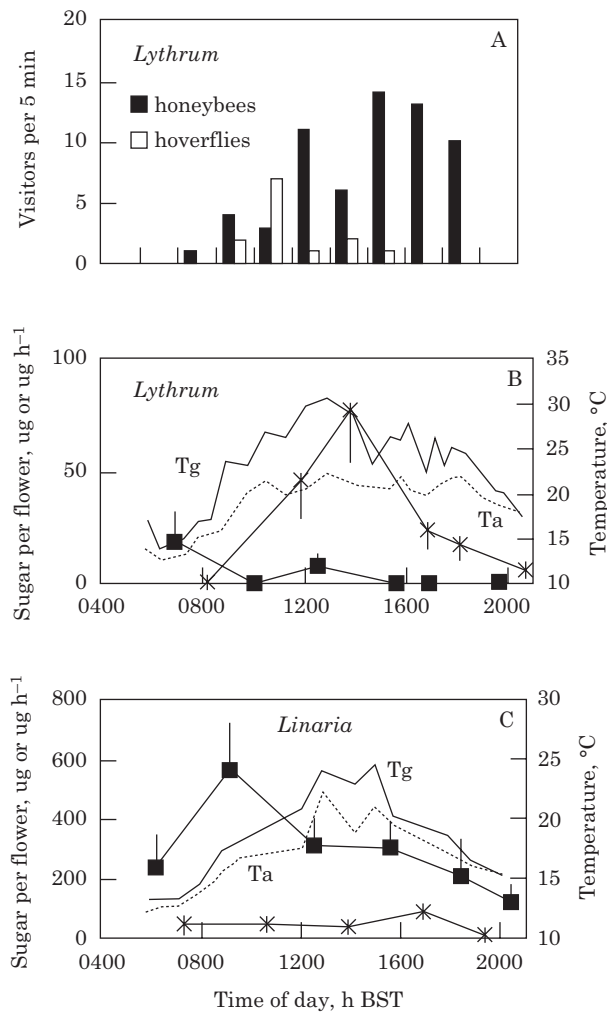


FIG. 3. Results of a dawn-to-dusk study of *Lythrum salicaria* on 19 Jul. 1998 (A, B) and *Linaria vulgaris* on 29 Jun. 1998 (C). Numbers of honeybees and hoverflies present or arriving per spike in 5 min periods are shown in A. Mean (and s.e.) nectar secretion rates (x,  $\mu\text{g}$  sugar per flower  $\text{h}^{-1}$ ) and standing crops (■,  $\mu\text{g}$  sugar per flower) are shown in B and C, with ambient (dotted line, Ta) and black globe (continuous line, Tg) temperatures. All plots share the same scale on the x-axis.

potentially accessible to even short-tongued insects (Fig. 4H, J), but the corolla of single soapwort is so deep that even the longest-tongued bumblebee species can probably reach nectar only by probing between calyx and petals (Fig. 4G, I). Since the bees would not necessarily contact the anthers and stigma, this is theft *sensu* Inouye (1983). We saw shorter-tongued bees taking nectar by robbing through holes bitten in the calyx (and see Comba *et al.*, 1999a). No insects were seen visiting single or double flowers on 23 July, except pollen beetles in the flowers and two honeybees (*Apis mellifera*) that probed briefly and apparently unsuccessfully from the mouth of single flowers. On other occasions, the only visitors seen probing from the mouth of single flowers were two *Bombus hortorum* and a red admiral butterfly [*Vanessa atalanta* (L.)]. Three *B. terrestris/lucorum* acted as primary and secondary robbers, taking nectar via a hole in the calyx. Four *Apis*

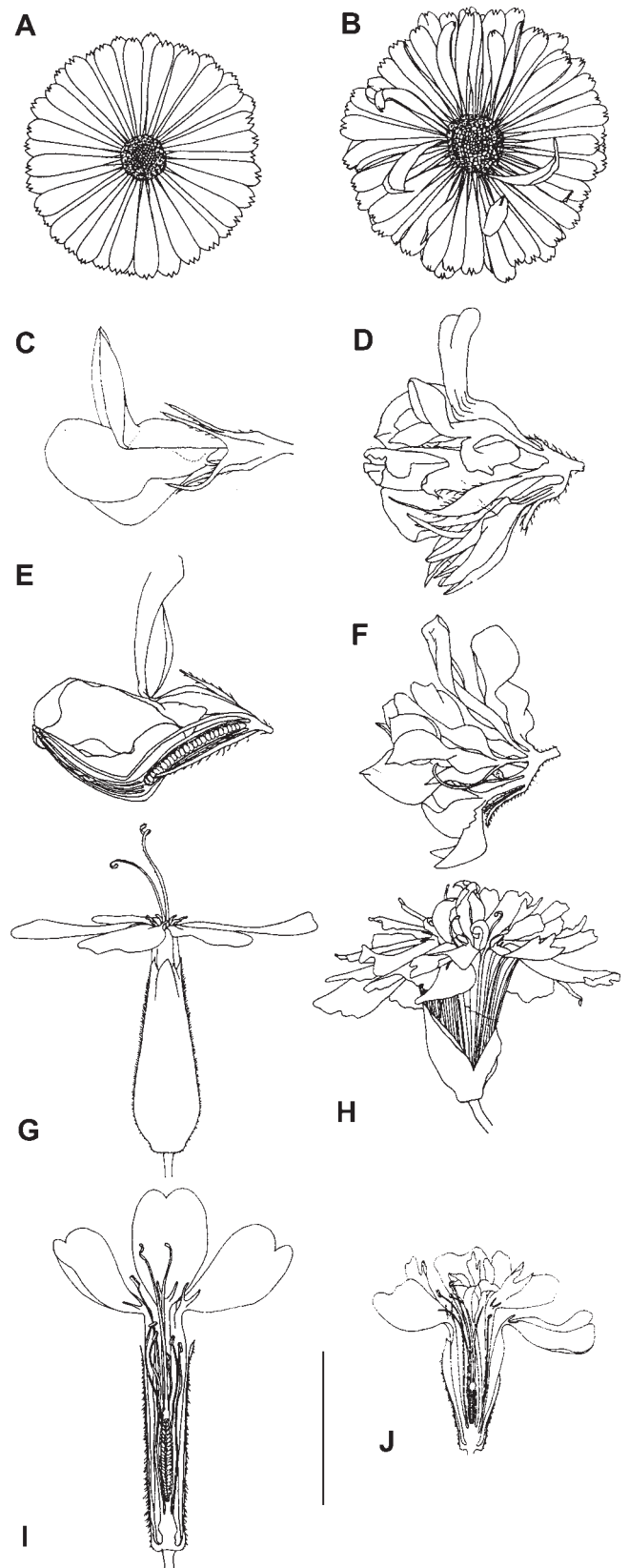


FIG. 4. Capitula of *Calendula officinalis* single (A) and double 'Orange King' (B); whole and half flowers of *Lotus corniculatus* single (C, E) and double (D, F), and *Saponaria officinalis* single (G, I) and double (H, J). Bar = 10 mm.



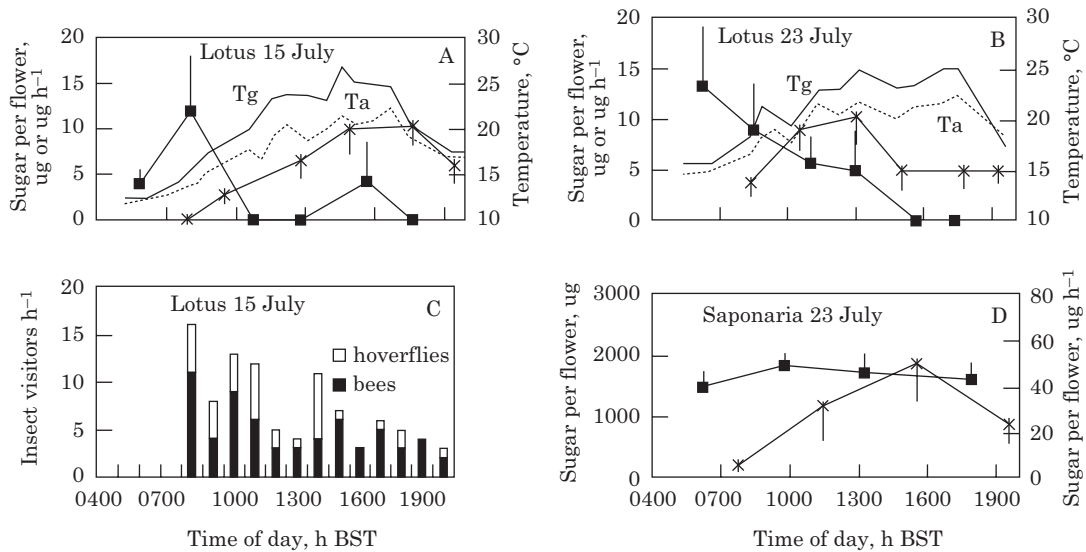


FIG. 5. Dawn-to-dusk studies of nectar (A, B, D) and insect visitors (C) to *Lotus corniculatus* (A–C) and nectar in *Saponaria officinalis* (D). Mean (and s.e.) standing crop of nectar sugar per flower (■) and secretion rate (x) in *Lotus* on 15 Jul. 1998 (A) and 23 Jul. 1998 (B), with air temperature (Ta) and black globe temperature (Tg); and mean (and s.e.) standing crop of nectar sugar per flower (■) and secretion rate (x) in *Saponaria* on 23 Jul. 1998. Because the standing crop was much higher than the secretion rate in *Saponaria*, standing crop and secretion rate are shown on different axes in D. C shows changes through the day in the numbers of bees (■) and hoverflies (□) foraging on *Lotus* on 15 Jul. 1998.

*mellifera* probed between the calyx and corolla from the top of the calyx. The rarity of such visits indicates that they may not have succeeded in reaching the very large standing crops of nectar in the flowers.

#### *Petunia* × *hybrida*

We studied three cultivars with flowers of a similar rose-purple colour: ‘Express Pink’ (a Grandiflora) and F1 ‘Pink Waves’ (a Multiflora hybrid), both of which have single flowers, and ‘Duo Rose’ (a Multiflora hybrid) that has double flowers (Fig. 6). The Grandiflora and Multiflora hybrids differed in corolla size. Bumblebees could push the front of the head down as far as the stamen bases. The distance from that point to the nectary, equivalent to the length of tongue required to reach small quantities of nectar, was  $7.9 \pm 0.1$  mm ( $n = 10$ ) in Grandiflora and  $6.1 \pm 0.3$  mm ( $n = 9$ ) in single Multiflora. This compares with a mean tongue length of  $6.6 \pm 0.1$  mm for honeybees,  $6.3 \pm 0.5$  mm for *Bombus lucorum*,  $7.9 \pm 0.5$  mm for *B. terrestris*,  $7.9 \pm 0.7$  mm for *B. pascuorum* Scopoli and  $12.4 \pm 1.0$  mm for *B. hortorum* (Corbet et al., 1995). Evidently nectar of single Multiflora should be accessible to honeybees and all bumblebee species recorded during our study, whereas nectar of Grandiflora can be reached only by *B. terrestris*, *B. pascuorum* and *B. hortorum*.

The double cultivar ‘Duo Rose’ had extra petals and about 20 stamens (compared with four stamens in single flowers). Stigmas and stamens were obscured by super-numerary petals (Fig. 6). Some of its anthers did not dehisce, and few of its stigmas matured.

Both single cultivars yielded nectar on both dates. The per-flower standing crop and secretion rate were sometimes marginally higher in single Multiflora than in Grandiflora (Fig. 7, Table 2), and as the single Multiflora cultivar had

more flowers per plant ( $24 \pm 2$  in Multiflora vs.  $15 \pm 1$  in Grandiflora,  $n = 10$  for each), it provided much more nectar per plant. Temperatures were higher on 18 June than on 30 June, as were the standing crops and secretion rates, which probably depend on temperature (Búrquez and Corbet, 1998). Measured solute concentrations were in the range 15–85% in Grandiflora and 14–85% in single Multiflora on 18 June, and 1–62% in Grandiflora and 1–53% in single Multiflora on 30 June. On 30 June, the weather was overcast with rain showers, and many sampled flowers contained large volumes of liquid (some exceeding 200  $\mu$ l) that gave concentration readings of 0% (indicating that the liquid withdrawn from the corolla was water) or less than 10% (indicating dilution of nectar by rain or dew). In flowers sampled for standing crop, these low concentrations were found in only about 2% of flowers on 18 June (2/70 Grandiflora and 1/70 single Multiflora), but on 30 June they were found in 30–80% of Grandiflora at all sampling times, and in 50% of sampled flowers of single Multiflora in the first two runs of the morning (before 0935 h).

The double cultivar ‘Duo Rose’ was sampled sporadically for standing crop on 30 June, although it was difficult to push the microcap through the densely-packed floral parts to the nectary region without causing damage. Most flowers yielded no nectar, and no sample contained a sugar content of more than 2  $\mu$ g or a solute concentration greater than 3%.

Like Darwin (1876), we saw few insects foraging on *Petunia* flowers. In eight monitoring sessions on 18 June, single Multiflora received two foraging visits from the bumblebee *Bombus terrestris/lucorum* (one taking nectar, one taking both nectar and pollen). Grandiflora received one foraging visit from *B. terrestris/lucorum*, which took nectar briefly. The cultivar ‘Duo Rose’ was visited by one

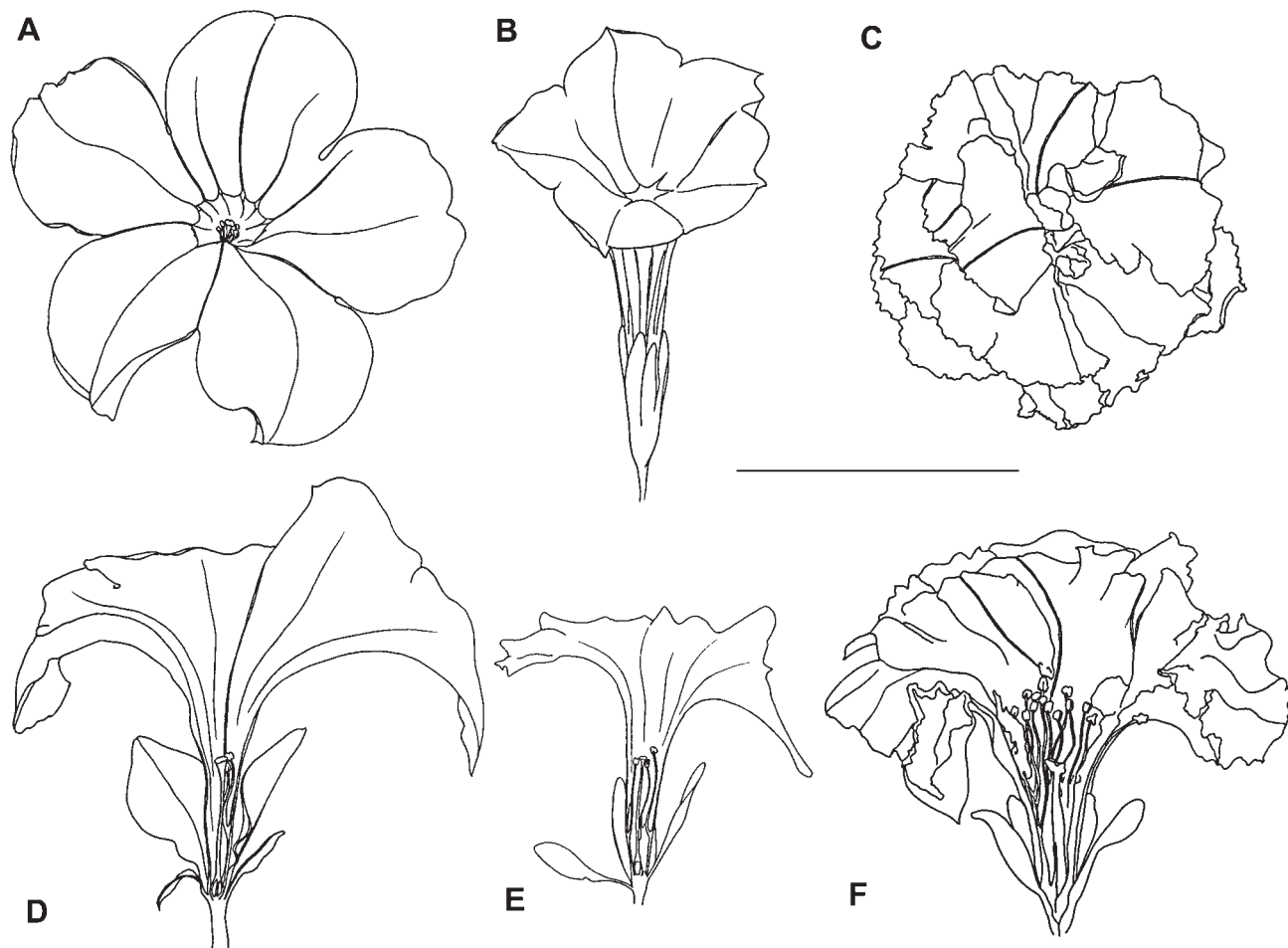


FIG. 6. Whole (A–C) and half (D–F) flowers of *Petunia* × *hybrida* ‘Express Pink’ (Grandiflora) (A, D), ‘Pink Waves’ (Multiflora) (B, E) and ‘Duo Rose’ (Multiflora) (C, F). Bar = 5 cm.

*B. hortorum*, apparently unable to probe between the many closely-packed petals. In the cooler weather of 30 June no foraging was seen: single Multiflora received brief non-foraging visits from two bumblebees (a *B. terrestris/lucorum* and a *B. hortorum*), one honeybee and two hoverflies; Grandiflora received one non-foraging visit from a *B. terrestris/lucorum*; and the double cultivar received no visits. Given the large numbers of flowers open on 18 June (1200 single Multiflora, 504 Grandiflora and 44 ‘Duo Rose’), a total of only three foraging visits over the day is a remarkably low visitation rate.

#### *Calendula officinalis*

Single pot marigold flowers had only one whorl of outer ray florets, whereas the nominally double cultivar we studied, ‘Orange King’, had several (Fig. 4). The disc florets are arranged in a spiral pattern on the capitulum, and over a period of days a wave of flowering moves inwards from the outer rim towards the centre. Capitula of the single type usually bore about three rings of open disc florets at any one time. The double cultivar had numerous

rings of disc florets open making it difficult to keep track of them all for measurement of nectar secretion rates.

Capitula showed a pronounced daily pattern of opening and closing, seen particularly clearly in the single type. At night the ray florets bent inwards to cover the disc florets and by day they re-extended so that the disc florets were exposed (Fig. 8). Such movements were less apparent in the double cultivar, in which nectar and pollen were therefore potentially available for longer each day.

The dawn-to-dusk study on 7 July showed that the standing crop of nectar sugar per ‘open’ (with disc florets exposed) capitulum was marginally higher in the double cultivar than in the single type around 1200 h (Fig. 9C, Table 2), possibly because of the larger capitula with more open disc florets per capitulum in the double ‘Orange King’. The standing crop of nectar sugar was low early in the morning, but rapid secretion (and/or recruitment of freshly-opened nectar-rich disc florets) elevated the standing crop per capitulum, so that around midday and early afternoon capitula of both types contained about 30–50 µg sugar. At this time insect visits were numerous (Fig. 9A). With a total of 1200 open capitula, the plot of single marigolds received more insect visitors per unit area, but the double, with only

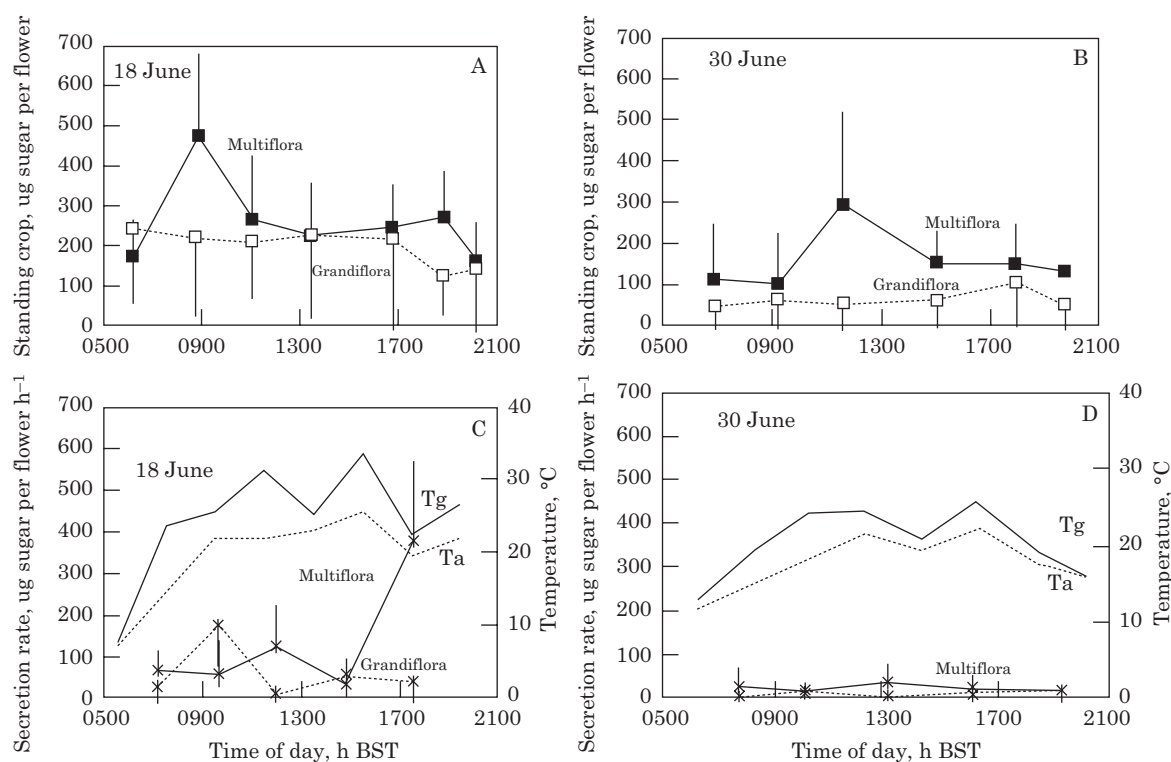


FIG. 7. *Petunia x hybrida*. Results of dawn-to-dusk studies on 18 June (A, C) and 30 Jun. 1999 (B, D), showing changes through the day in mean (and s.e.) standing crop (■, □, A, B) and secretion rate (x, C, D) of nectar in single Multiflora (—■—) and Grandiflora (—□—). Double flowers secreted virtually no nectar. Ambient (Ta) and black globe (Tg) temperatures are shown in C and D.

220 open capitula in the plot, usually received more visitors per capitulum (Fig. 9). At the time of our study, the single had more open flowers per plant than the double [ $28 \pm 2$  ( $n = 10$ ) vs.  $3 \pm 0.4$  ( $n = 10$ ) respectively].

Single and double pot marigolds hosted a similar range of visitors, many of which took pollen as well as nectar. Among them were small solitary bees of the genus *Lasioglossum*, including *L. morio* (Fabricius) and *L. calceatum* (Scopoli) (Fig. 9B). Other bees included *Apis mellifera* L., *Bombus lapidarius* (L.), *B. pratorum* (L.), *B. terrestris/lucorum* and *Megachile willughbiella* (Kirby). Hoverflies, relatively few on this occasion, included *Episyrphus balteatus* (De Geer), *Platycheirus albimanus* (Fabricius), *Eristalis tenax* (L.), *Eupeodes luniger* (Meigen) and *Merodon equestris* (Fabricius). Flight activity of hoverflies and small bees depends on the weather as well as on resource availability (Heinrich, 1993). The insect feeding visitor counts through the day showed a closer correlation with black globe temperature (Pearson correlation coefficient 0.778,  $P = 0.001$ ,  $n = 14$ ) than with air temperature (0.611,  $P = 0.02$ ,  $n = 14$ ).

## DISCUSSION

Rates of nectar secretion vary widely with plant species, and within a species they vary from day to day (Table 2) and from hour to hour (Figs 1–3, 5, 7, 9). Associated with variation in rates of secretion, reabsorption, and depletion by insects is variation in the standing crops of nectar present in the flowers (Table 2, Figs 1–3, 5, 7, 9). Our study

illustrates temporal variation, but does not show the full range of species-dependent variation. All the native British species examined here were selected for their large, colourful flowers, such as might appeal to gardeners. Species with large flowers are often perennials with high rates of nectar secretion (Corbet, 1995), and all the British species studied offer rich nectar rewards, with maximal mean secretion rates ranging from about 20 to 90  $\mu\text{g}$  sugar per flower  $\text{h}^{-1}$  and maximal mean standing crops ranging from about 10 to 600  $\mu\text{g}$  sugar per flower (Table 2). With the possible exception of *Linaria*, they were all visited by substantial numbers of insects, including bumblebees and honeybees. All but *Lythrum* had deep enough flowers for long-tongued species of bumblebee such as *B. hortorum* and *B. pascuorum*. Among the native species, *Lythrum*, with the shortest corolla, had a high rate of depletion by relatively short-tongued insects, and a correspondingly low standing crop. *Linaria*, with the longest corolla and a relatively low rate of depletion by insects, had the highest standing crop.

As ornamental native British plants offering nectar that can help to support valuable long-tongued pollinators such as *Bombus pascuorum* and *B. hortorum*, we have already recommended *Silene dioica* (L.) Clairv., *Silene latifolia* Poir., *Lychnis flos-cuculi* L., *Stachys palustris* and *Stachys sylvatica* L. (Comba et al., 1999a). To that list we now add *Salvia pratensis*, *Stachys officinalis*, *Lotus corniculatus* and *Linaria vulgaris*. As in our earlier study, the species of *Stachys* were also visited by the interesting solitary bee *Anthidium manicatum*. *Malva moschata* L., *M. sylvestris* L.

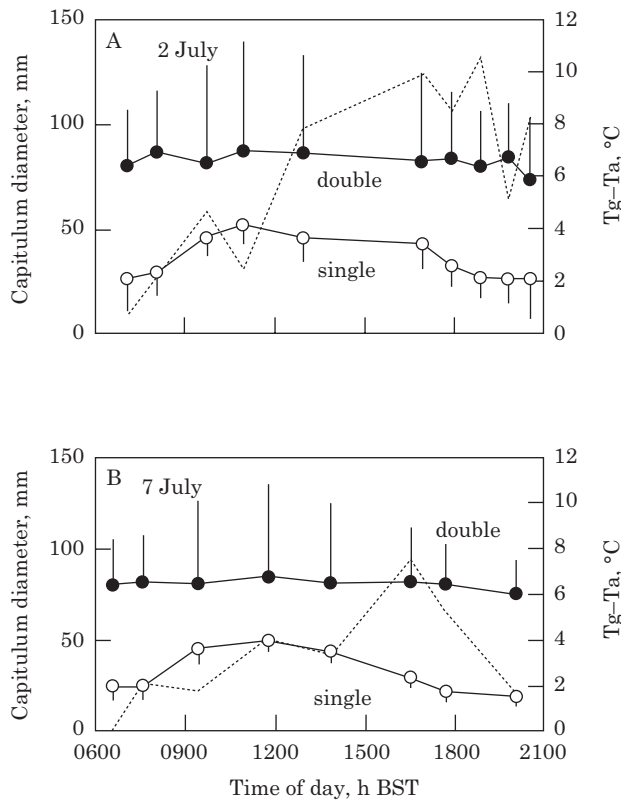


FIG. 8. *Calendula officinalis*. Changes through the day in mean ( $\pm$ s.e.) capitulum diameter of single (○) and double (●) flowers on 2 Jul. (A) and 7 Jul. 1999 (B). The dashed line shows the difference between ambient and black globe temperature, an index of incident radiation that commonly correlates with floral movements (Corbet, 1990).

and *Lythrum salicaria* are also ornamental and nectar-rich, and their more open flowers attract a different spectrum of insect species, with more short-tongued forms including solitary bees and hoverflies. As shown elsewhere (Comba et al., 1999a), *Lythrum* also attracts numerous butterflies in the appropriate season.

The alien species we studied fall into two categories: the neotropical *Salvia splendens* and *Petunia*  $\times$  *hybrida*, and the temperate-zone *Saponaria officinalis* and *Calendula officinalis*. The two neotropical species produced abundant nectar, but received very few insect visits. *Salvia splendens* had a higher rate of secretion than any of the British species and, in the absence of hummingbirds—thought to be its coevolved pollinators—much of the nectar remained unexploited. The Cambridge fauna evidently lacked any bird or insect visitors with correspondingly long tongues. In an earlier study, another neotropical hummingbird flower with more accessible nectar—nasturtium, *Tropaeolum major*—did receive visits from long-tongued bumblebees (Comba et al., 1999b).

Single cultivars of *Petunia*  $\times$  *hybrida* provided nectar, and the potential value to insects was greater in the single Multiflora hybrid than the Grandiflora hybrid because the former contained more nectar per plant and had smaller flowers, making the nectar accessible to a wider range of

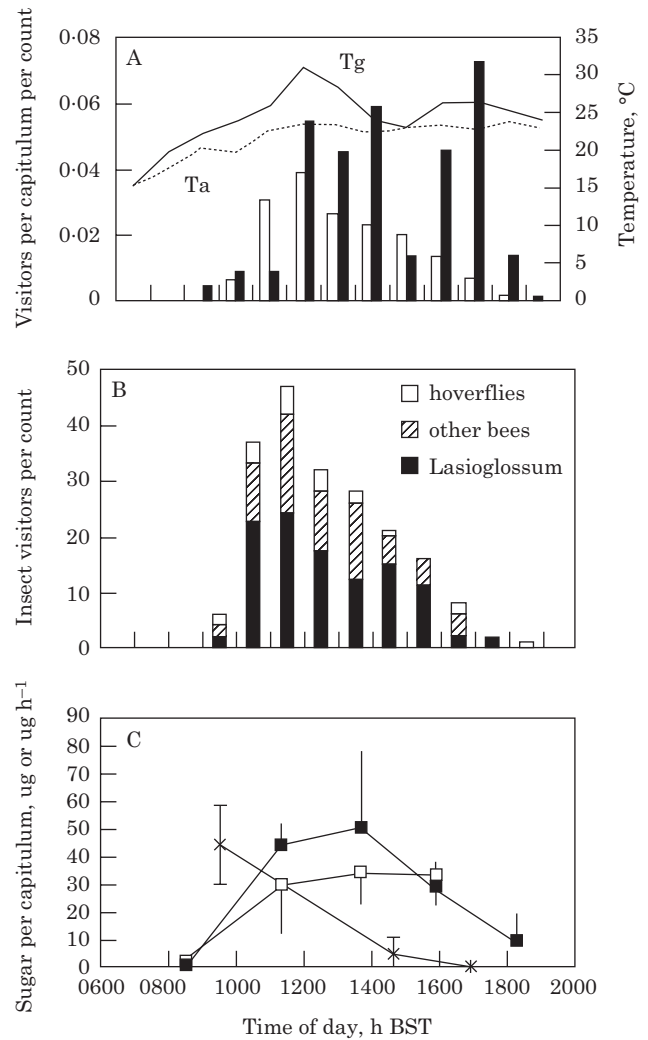


FIG. 9. *Calendula officinalis*, 7 Jul. 1999. A, Numbers of insect visitors per capitulum seen feeding on the flowers of double (■) and single (□) marigolds, with air temperature (Ta) and black globe temperature (Tg). B, Total numbers of *Lasioglossum* (■), other bees (▨) and hoverflies (□) seen feeding on single marigolds. C, Standing crop of nectar sugar in disc florets per capitulum (mean and s.e.) on single (□) and double (■) marigolds, and secretion rate (x) in single marigolds.

insects including shorter-tongued species. Further, it was less liable to dilution of nectar by rain or dew.

We did not monitor insect visits to *Petunia*  $\times$  *hybrida* throughout the night, and the possibility that moths visit the flowers remains to be explored. Like Darwin (1876), we found that even the nectar-rich single variants received very few insect visits by day. Why? Social bee species present on the site had tongues long enough to reach the nectar, particularly in the single Multiflora hybrid, and numerous insects were visiting other flowers nearby, including the long-tongued *Bombus hortorum* on *Aconitum napellus*. On 30 June 1999, rain accumulating in the upward-facing flowers diluted the solutes in most flowers of Grandiflora and many of the single Multiflora to a level well below that on which bees normally forage. But a further explanation is required because visits were also few on 18 June when

solute concentrations were in an acceptable range. Perhaps *Petunia* nectar contains deterrent secondary metabolites, like that of *Catalpa speciosa*, in which iridoid glycosides deter visits by unadapted nectarivores but not by legitimate pollinators (Stephenson, 1981, 1982).

Of the two temperate-zone aliens, *Saponaria officinalis* is probably native in Central and Southern Europe (Blamey and Grey-Wilson, 1989), and probably introduced in Britain (Stace, 1997); while *Calendula officinalis* is of unknown origin, but members of the genus occur in the Mediterranean and Macaronesia (Huxley, 1992). Thus in their native regions both species would encounter a range of insect species broadly similar to those in Britain.

Pot marigolds offered nectar and pollen to a wide range of insect visitors, including several species of relatively short-tongued bees and hoverflies. Our findings support the recommendation to plant pot marigolds to support flower-visiting insects that are natural enemies of pests.

Few insects visited *Saponaria*, and large standing crops of nectar accumulated in the single flowers, with a greater volume (mean  $5.3 \pm 0.4 \mu\text{l}$ ) and lower solute concentration ( $31.1 \pm 1.6\%$ ,  $n = 40$ ) than Witt et al. (1999) found in plants in a growth chamber. The corolla is so deep that shorter-tongued insects cannot secure the nectar via the mouth of the flower, and even the longest-tongued bumblebee species can probably reach nectar only by probing between calyx and petals. Since the bees would not necessarily contact the anthers and stigma, this is termed theft by Inouye (1983). We saw shorter-tongued bees robbing nectar through holes bitten in the calyx (and see Comba et al., 1999a), but we saw no hawkmoths, which are probably rare in our urban study site. The double flowers secreted little or no nectar, and no insects were seen taking nectar or pollen from them.

### Doubles

Single birdsfoot trefoil (*Lotus corniculatus*) yielded nectar and pollen which were well exploited by insects, including some long-tongued bee species. The double form apparently provides no nectar or pollen, and no insects were seen visiting it during this study.

Whereas the single cultivars of *Petunia* × *hybrida* contained nectar, the double cultivar ‘Rose Duo’ contained virtually none and no insects were seen foraging on it successfully. It was apparently valueless to insects, secreting little or no nectar and producing little or no pollen when its anthers failed to dehisce. On the one occasion when a bee was seen to visit it, the extra petals seemed to obstruct probing.

The Asteraceae represent a special case because doubling may not alter the structure of individual florets, but may simply change the relative proportions of disc florets and ray florets. This was so in *Calendula*, in which enlargement of the capitula in the double form ‘Orange King’ compensated for the lower proportion of disc florets, so that doubles and singles yielded similar standing crops of disc floret nectar sugar per capitulum. The double cultivar received more insect visits per capitulum, but fewer in total because it bore fewer open capitula per plant than the single

form. Similarly in another member of the Asteraceae, the French marigold *Tagetes patula*, double and single variants yielded similar standing crops of nectar per capitulum, but the single had more capitula per unit area (Comba et al., 1999b). Thus in the Asteraceae *Tagetes* and *Calendula*, some degree of floral doubling may have little effect on the quantity of nectar per capitulum or the numbers of insect visits per capitulum, especially where it is associated with an increase in capitulum size.

Except in the Asteraceae, floral doubling may suppress nectar secretion (*Lotus*, *Petunia*, *Saponaria*), especially if it involves loss of a functional spur (*Tropaeolum*, *Consolida*) (Comba et al., 1999b), and altered flower structure modifying the morphological fit to the pollinator (e.g. reduced effective corolla depth in double *Lotus* and *Saponaria*) and obstructing probing (*Petunia*, *Consolida*) (Reynold and Tampion, 1983). Generally, these double flowers were of little value to insects.

The selected range of plant species studied here and by Comba et al. (1999a, b) are nectar-rich. Some double variants produce little or no nectar and, together with some species from countries with a fauna different from our own, they receive few insect visits. Gardeners seeking to enhance pollinator populations are encouraged to grow selected native species and single variants where possible. If double variants and exotic species are to be grown, they should be chosen with caution.

### ACKNOWLEDGEMENTS

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