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Honesty of signaling and pollinator attraction: The case of flag-like bracts

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ABSTRACT

Bracts are nonfloral showy structures associated with inflorescences. They are generally thought to enhance plant reproductive success by attracting pollinating insects. We investigated whether flag-like bracts at the top of inflorescences are reliable signals of floral food reward for pollinators in *Salvia viridis* L. Field and greenhouse data indicate incomplete synchrony between the development of flowers and bracts. Various measures of bract size, however, positively correlate with the number of open flowers on the inflorescence, and with their nectar rewards. Experimental removal of bracts from inflorescences significantly reduced honeybee visitation in the field. We compare these findings with field data on *Lavandula stoechas* L., another labiate species with flag-like displays. The number of open flowers in *L. stoechas* cannot be reliably predicted from the presence or size of the bracts. Bract clipping does not significantly reduce honeybee visits in this species. We suggest that bees learn to orient to bracts if they reliably signal food rewards and to disregard bracts if they provide unreliable signals. Asynchronous development of bracts and floral rewards can reduce the reliability of the signals and may explain the rarity of flag-like displays in pollination systems. We discuss additional selective forces that may favor bract displays.

Keywords: flag-like bract, extra-floral display, pollination ecology, signaling, honeybee, phenology, *Salvia*, *Lavandula*

INTRODUCTION

The evolution of many floral traits is shaped by the foraging behavior of their insect pollinators (Faegri and van der Pijl, 1979). Pollinators perceive and learn to respond to many features of flowers, such as colors, odors, symmetry, or nectar guides (Giurfa and Lehrer, 2001). These features are considered display cues, which advertise the plant's presence, and/or its quality as a food resource, to potential pollinators. The presence and intensity of the display cues generally correlate positively with nectar and pollen rewards, providing honest advertising (Chittka and Thomson, 2001). Infrequent cases of deception, i.e., non-rewarding flowers with conspicuous displays, presumably involve food mimicry or sexual mimicry (Dafni, 1984; Gigord et al., 2002; Schiestl, 2004).

Colored visual display organs other than flowers are known in many plant species (Heywood, 1978; Proctor et al., 1996). They can be divided into two groups: colored organs that encircle the flowers (e.g., *Bouganvillea*, *Statice*, and *Limonium*), and flag-like organs that extend as colorful appendages at the top of inflorescences. Accessory bracts of both groups have been repeatedly hypothesized to provide signals to pollinating insects as

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to the location of flowers (Muller, 1873; Knuth, 1898; Grant and Grant, 1964; Meeuse and Meeuse, 1984; Barth, 1985). Bracts were suggested to be very efficient displays, since one large signaling structure, conspicuous from afar, can advertise many flowers on an inflorescence (Faegri and van der Pijl, 1979; Gottsberger and Hartmann, 1988). Arguably, having more flowers per inflorescence is a simple way to produce large visual displays, which does not require extra-floral display organs. However, such inflorescences may suffer from increased selfing rates through geitonogamy.

Surprisingly, rather few studies attempted to study the advertising role of bracts, and these attempts yielded equivocal results. Bract clipping in a Spanish population of *Lavandula stoechas* slightly reduced pollinator visitation rates and seed sets, but the effect was generally statistically insignificant (Devesa et al., 1985; Herrera, 1997). The removal of bracts from *Mussaenda frondosa* L. inflorescences reduced pollination visits by butterflies, but not by bees and birds (Borges et al., 2003). Both studies share a common trend, namely, some reduction in plant reproductive success following bract removal. This trend is consistent with the hypothesis that bracts function as advertising organs. In both studies, however, the effects of bract removal were rather modest and depended on experimental protocol and types of pollinators observed. The nonsignificant effects were attributed to small sample sizes and large variance among plants, which possibly obscured the effects of the bract removal treatment (Herrera, 1997). This interpretation may be limited by lack of information on the correlation between the bract display and the plants' value as food sources. The role of bracts as advertising organs may depend on the reliability of the signal they provide to pollinators as to plant or flower quality, since pollinators may orient mainly to bracts that reliably signal food rewards (Armbruster et al., 2005). Thus, extra-floral displays that dependably predict floral food rewards may be attractive to pollinators, while displays that are poor predictors of floral rewards may be unattractive.

In the present study we explore the correlations between extra-floral displays, pollinator visitation, and floral food reward in two plant species. We focus on the extra-floral displays provided by flag-like bracts. In line with previous studies, we hypothesize that flag-like bracts can function as advertising structures that attract pollinators. We extend this idea and further hypothesize that the effectiveness of this advertisement depends on its reliability. In other words, extra-floral displays may not provide a reliable foraging signal to pollinators in all plant species or populations. This could occur if display development is not well synchronized with the development and opening of flowers on the inflorescence. In such cases, pollinators should be selected (genetically, or through learning) to disregard the extra-floral signals, and orient to visual or chemical cues originating from the flowers. Pollinators may orient to extra-floral displays, on the other hand, if they honestly advertise the presence of flowers in the inflorescence.

We tested this hypothesis in natural populations of two species with flag-like bract displays in Israel, *Salvia viridis* and *Lavandula stoechas*. We tested whether removal of the flag-like bracts reduced visitation by honeybees. We then assessed the correlation between the extra-floral display and food rewards by studying the plant's flowering phenology in potted plants (for *S. viridis*) or in the field (for *L. stoechas*). We focused on the following questions in each plant species: (1) Are the flag-like bracts effective display cues, i.e., do they attract pollinators? (2) Are the flag-like bracts dependable display cues, that is, do they reliably signal food rewards to pollinators?

METHODS

We sampled bract frequency, monitored flowering phenology, and manipulated extra-floral displays in *Salvia viridis* and *Lavandula stoechas*. Bract frequencies were sampled in natural populations for both species. *S. viridis* phenology was observed in potted plants, while *L. stoechas* phenology was recorded in the field. Manipulations consisted of clipping of selected bracts in the field and recording subsequent pollinator visits. Clipping and observation protocols were not identical for *S. viridis* and for *L. stoechas*. We therefore describe below the detailed study protocol for each plant species separately.

Study plants

Salvia viridis (Lamiaceae) is a common annual in Mediterranean and Irano-Turanian grasslands, up to 40 cm tall. It forms dense patches that bloom (in Israel) between March and May. The protandrous flowers are arranged in whorls around the stem, and flowering progresses from the bottom of the inflorescences upwards. The upper lip of the corolla is dark purple while the lower lip is light purple or white. Corolla length is 15–18 mm (Feinbrun-Dothan, 1978; Alon, 1990). The species is polymorphic with respect to bracts, since they do not develop in all individuals. In fact, bracted and bractless morphs were previously considered separate species (Davis, 1982; Meikle, 1985). The frequency of the two morphs differs among populations. Flag-like bract clusters, composed of several colorful (purple, pink, or white) leaves, develop at the top of inflorescences. The first bract clusters usually develop on the

main inflorescence. In some cases, secondary inflorescences that develop later carry bract clusters as well.

Lavandula stoechas L. is a perennial, aromatic, xerophytic shrub of Mediterranean distribution that blooms between January and May (Feinbrun-Dothan, 1978; Herrera, 1993). Flowers are protandrous and are usually non-selfing and insect-pollinated (Devesa et al., 1985). Flowers have a small (5-mm long), dark-purple tubular corolla inserted into a tubular calyx, and are aggregated in heads. These are composed of tightly packed groups of flowers attached to a central common axis. In preliminary observations, we determined that 15.0 ± 8.3 (mean ± SD, n = 58) flowers bloom simultaneously per inflorescence, and that mean flower longevity is 4.61 ± 1.54 (SD) d (n = 70). The mean number of inflorescences per shrub is 117.5 ± 87.9 (mean ± SD, n = 30) at peak blooming. Many inflorescences are terminated by a tuft of 4–6 pink bracts. Mean inflorescence length is 22.0 ± 5.9 mm (SD, n = 100), and mean length of the bract cluster is 7.0 ± 5.9 mm (SD, n = 85). Thus, bracts account for about a third of total inflorescence size. These measurements agree well with data obtained for *L. stoechas* populations in Spain (Devesa, 1985; Gottsberger and Hartmann, 1988).

Study sites

The main field site for *S. viridis* was the Ruhama nature reserve, in the southwest of Israel. The area is characterized by phrygana vegetation dominated by *Thymelea hirsuta*, *Hyparrhenia hirta*, and *Coridothymus capitatus* growing on loess soil. Honeybees and solitary bees dominate the pollinator fauna. *S. viridis* forms large patches, made conspicuous by purple bracts, in the reserve.

Lavandula stoechas was studied at an open natural vegetation area near Harutzim in central Israel. The soil at the study site is red sandy loam and the vegetation is a mosaic of annual pasture patches and tall phrygana. The perennial vegetation is dominated by *Cistus salviifolius* and *Cistus creticus*, accompanied by *Calycotome villosa* and *Thymelaea hirsuta*. Honeybee hives were located 200 m from the research site. Honeybees accounted for more than 99% of the pollinator visits observed. The remaining pollinators were solitary bees (*Eucera* sp., *Nomada* sp.), wasps (*Polystes* sp.), beetles (*Oxythyrea*), moths (*Zygaena*), and two unidentified heteropterans.

Field sampling of bract frequency

We sampled the prevalence of bracts on flowering *S. viridis* plants in four natural populations of *S. viridis* in northern (Brosh), central (Pura), and Southern (Dorot, Ruhama) Israel in 2000 and 2001. For the Ruhama population, we also recorded the frequency of inflorescences that carried bracts without flowers. The prevalence of bracts in *L. stoechas* was sampled near Harutzim in central Israel in 1990.

Phenological observations—*S. viridis*

We used field-collected *S. viridis* seeds to produce 51 potted plants, grown under greenhouse conditions, in 2000. Seeds produced by these plants were used to grow 16 additional shrubs in 2001. We recorded the lengths of all bracts, the number of leaves per bract cluster, and the number of bracts per plant as measures of display intensity. We recorded the total number of flowers per plant, and determined nectar volumes in samples of flowers as indicators of the plant's food reward. We measured nectar volumes in samples of six flowers per inflorescence, taken from the bottom (two flowers), mid-height (two flowers), and top (two flowers) of the inflorescence. All parameters were recorded at 3-day intervals during the plants' two-month flowering period. In 2001, we recorded the presence of bracts and of flowers in 16 plants once a day to obtain precise data on the degree of synchrony between them.

Phenological observations—*L. stoechas*

We conducted weekly counts of the number of blooming inflorescences in a sample of thirty shrubs at the Harutzim study site to characterize the time course of blooming. We counted the number of open flowers in 60 inflorescences three times a week throughout the blooming period.

We registered the dates of appearance and wilting of the bracts in 100 marked inflorescences. One inflorescence broke during the study period. Data from the remaining 99 inflorescences were used for analysis. We recorded blooming dates for these inflorescences, i.e., the dates of opening of the first flower, and of wilting of the last flower of the inflorescence. These records provide information on the extent of synchrony between flower and bract cluster development.

Bract manipulation experiments—*S. viridis*

Experiments were conducted on three days in the spring of 2001. In all experiments, we clipped all bracts from *S. viridis* inflorescences. We recorded the number of arrivals of unmarked honeybees to manipulated inflorescences and to an equal number of intact control inflorescences. Since bees generally visited more than one flower per inflorescence, we also recorded the total number of visits to flowers on clipped and unclipped inflorescences. We followed each bee until it left our experimental patches. We used the total number of visit sequences to estimate the number of visiting individuals. This is probably an overestimate, since some individu-

als most likely visited the experimental patches more than once during the observation periods. Visits were recorded by two observers immediately after bract cluster removal, simultaneously for manipulated and control inflorescences. We used three bract cluster removal treatments, as detailed in Table 1: (a) "Patch" treatment, where we clipped bract clusters from a whole patch; (b) "Binary" treatment that involved removal of half of the bract clusters within a patch at random locations; and (c) "Split" treatment, in which we clipped all bract clusters from one half of a patch and left its other half intact. In one of the "patch" treatments we clipped and reattached all bract clusters in the control patch, while bract clusters in the manipulated patch were clipped and removed ("clipped control", Table 1). This was done to control for the possibility that odors emanating from clipped inflorescences deter pollinators.

We determined nectar volumes in a sample of flowers from manipulated and control inflorescences in eight replicates to test for possible effects of clipping on floral reward levels. We used 1-μl microcapillaries for nectar sampling. Sample sizes for nectar measurements are provided in Table 1.

Bract manipulation experiments—*L. stoechas*

Experiments were conducted during nine days in the spring of 1990. As in *S. viridis*, we compared pollinator activity on intact infloresences vs. inflorescences from which bract clusters had been experimentally removed. We created two bract cluster removal treatments. In the "Plant" treatment, we clipped bract clusters at the bud stage from all inflorescences of treated plants, creating plants that bore no bracts throughout the blooming season. In the "Inflorescence" treatment, we clipped bract clusters from haphazardly determined inflorescences just before observation sessions. This created plants that contained mosaics of bracted and bractless inflorescences (Table 2). We set up these treatments to control for the possibilities that (a) pollinators can memorize the locations of bracts (and orient to these locations) even after the bracts are no longer there, and (b) a large concentration of bract clusters increases pollinator attraction. If these possibilities are valid, then pollinators are expected to discriminate against clipped inflorescences in the "Plant" treatment, but not in the "Inflorescence" treatment. We recorded the number of pollinator arrivals to manipulated and control inflorescences simultaneously in 10-min observation sessions.

Data analysis

We calculated the proportion of sampled inflorescences that bore both flowers and bracts, flowers without bracts, and bracts without flowers, in both study species. In *S. viridis*, we used linear regressions to relate bract display parameters (bract cluster length, number of leaves per bract cluster, number of bract clusters per plant) to reward parameters (number of flowers, mean nectar volume per flower). We used each plant's measurements of display and reward on the day of maximal bract cluster length for analysis. Thus, each plant in the sample contributed a single data point to the regression. This analysis was not performed for *L. stoechas* since bract clusters did not change in size during the blooming period.

In the bract removal experiments, we scored the proportion of replicates that had more bee visits to intact

Table 1
Details of bract manipulations and nectar sampling in the *Salvia* experiments

Pattern of bract removal	Replicate	No. inflorescences observed (manipulated + control)	Duration of observation (min)	No. flowers for nectar sampling, manipulated	No. flowers for nectar sampling, control
Patch, clipped control	1	180	180	32	37
Patch	2	170	110	29	33
Patch	3	120	120	19	24
Patch	4	15	50	—	—
Patch	5	15	140	—	—
Patch	6	55	45	—	—
Binary	1	50	30	25	22
Binary	2	122	60	11	17
Binary	3	120	50	35	24
Split	1	50	30	19	25
Split	2	100	60	34	31
Split	3	120	50	—	—

Table 2

Pollinator activity in *L. stoechas* bract manipulation experiments. "Plant" and "Inflorescence" treatments differ in the protocol of bract clipping (see Methods). We report the mean number of pollinator arrivals, and the mean number of flowers visited per inflorescence in a standard 10-min observation period. NR—not recorded. Cases of lower pollinator activity in manipulated inflorescences than in controls are marked in bold. All pollinators were honeybees, except in replicates 2, 3 in treatment "Inflorescence" (some visits by *Eucera* sp.) and replicate 8 in treatment "Inflorescence" (one visit by *Oxythyrea* sp.)

a. Treatment "Plant"

Replicate	No. inflorescences observed		No. pollinator arrivals		No. flowers visited	
	Clipped	Control	Clipped	Control	Clipped	Control
1	86	161	NR	NR	0.558	0.509
2	56	45	NR	NR	1.050	0.490
3	55	68	NR	NR	**0.600**	**1.260**
4	67	42	NR	NR	**0.630**	**1.190**
5	95	28	**0.042**	**0.178**	**0.378**	**0.714**
6	87	57	**0.149**	**0.333**	**0.632**	**1.400**
7	53	29	**0.472**	**0.724**	**1.940**	**3.370**

b. Treatment "Inflorescence"

Replicate	No. inflorescences observed		No. pollinator arrivals		No. flowers visited	
	Clipped	Control	Clipped	Control	Clipped	Control
1	71	56	**0.098**	**0.107**	NR	0.839
2	26	28	0.385	0.357	**1.269**	**1.428**
3	26	28	**0.192**	**0.285**	**0.423**	**1.178**
4	26	28	0.692	0.321	2.730	1.320
5	29	26	**0.172**	**0.423**	**1.000**	**1.460**
6	43	28	**0.023**	**0.214**	**0.093**	**0.928**
7	32	40	**0.063**	**0.125**	**0.312**	**1.050**
8	73	124	**0.041**	**0.048**	0.465	0.177
9	73	107	0.109	0.037	1.315	0.336
10	49	29	0.082	0.068	**0.489**	**0.621**
11	49	29	0.184	0.000	0.979	0.000

Table 3

Proportion of blooming *S. viridis* inflorescences that bore bracts

Population	No. plants sampled	Proportion of blooming inflorescences with bracts
Brosh	150	0.99
Pura	150	1
Dorot	150	1
Ruhama	245	0.89
Greenhouse	67	0.98

inflorescences than to clipped inflorescences. We tested the hypothesis that this proportion was higher than 0.5 using one-way sign tests. We employed Wilcoxon paired-sample tests to examine whether mean parameters of bee visits were higher in control inflorescences than in their manipulated counterparts.

RESULTS

S. viridis

The prevalence of bracts and bract-flower synchrony

Blooming inflorescences bore bracts in almost all plants sampled in field populations, and in potted plants in the greenhouse (Table 3). In the Ruhama population, 23% of the sampled inflorescences bore bracts but no open flowers, suggesting incomplete synchrony between flowering and the development of the potential advertising signal. In potted greenhouse plants, bracts developed 9.47 ± 1.70 d (mean ± SE, n = 17) before the blooming of the first flowers, and wilted 2.00 ± 1.29 d after the last flowers of the inflorescence. Bracts preced-

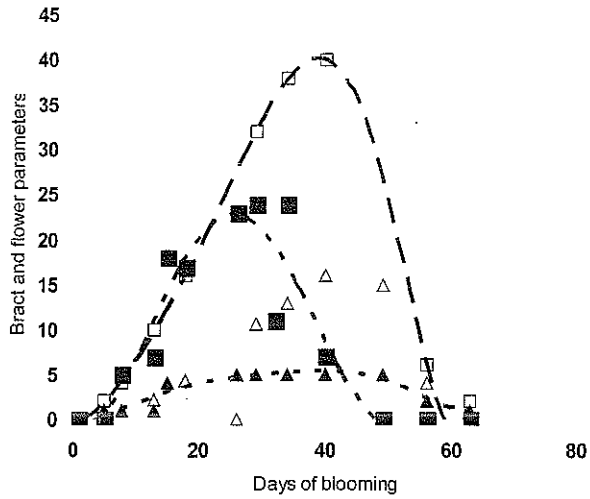

Fig. 1. Representative time course of blooming and bract cluster development in an *S. viridis* inflorescence. ■—number of flowers, □—number of bracts, ▲—number of bract clusters, △—bract cluster length (cm). Best-fit curves are based on 6th-order polynomials.

ed flowers in 94% of this 17-plant sample, and remained on the plant after the flowers had wilted in 29% of the plants in the sample.

Bract cluster size and reward parameters

The number of flowers first increased, then decreased during the blooming period. Plants developed secondary inflorescences during the flowering period. Since secondary inflorescences often bore bracts, the number of bract clusters per plant changed during the flowering period as well. Bract clusters increased in length through the addition of leaves, and decreased in length when some of these leaves wilted. A typical time course for the changes in flower number, bract cluster number, bract cluster length and number of leaves per bract cluster is provided in Fig. 1.

Bract cluster length was significantly and positively correlated with the number of flowers per inflorescence ($n = 65$, $r^2 = 0.31$, $p < 0.0001$) and nectar volume per flower ($n = 65$, $r^2 = 0.31$, $p < 0.0001$). Flower number and nectar content also correlated positively with the number of bract clusters ($n = 65$, $r^2 = 0.14$, $p < 0.0001$ and $r^2 = 0.19$, $p = 0.002$, respectively) and with the number of leaves per bract cluster ($n = 65$, $r^2 = 0.13$, $p = 0.002$ and $r^2 = 0.19$, $p = 0.001$, respectively).

Bract manipulation experiments

Honeybees visited fewer flowers in manipulated inflorescences than in untreated control plants in ten out of twelve experiments (all three treatments were pooled). In these ten experiments, the number of arrivals at control inflorescences was also higher than at bractless inflorescences (Table 4). The occurrence of the same pattern in ten out of twelve cases is unlikely to result from a random process (sign test, $n = 12$, $Z = 2.02$, $p = 0.04$). The number of bees in control patches was higher than in manipulated patches in eight out of eleven replicates (the number of bees was not recorded in replicate no. 3), i.e., not more frequently than expected at random. We pooled the twelve replicates from different treatments and calculated the difference between treatment and control in the number of arrivals at inflorescences, visits to flowers, and number of bees. The significance of the difference was 0.058 ($Z = 1.57$, $n = 12$) for arrival at inflorescences, 0.050 ($Z = 1.65$,

Table 4
Pollinator activity in *S. viridis* bract manipulation experiments. Cases of lower pollinator activity in manipulated inflorescences than in controls are marked in bold. NR—not recorded

Pattern of bract removal	Replicate	No. flowers visited		No. inflorescences visited		No. bees	
		Control	Manipulated	Control	Manipulated	Control	Manipulated
Patch, clipped control	1	**499**	**326**	**384**	**157**	**19**	**18**
Patch	2	**335**	**185**	**239**	**143**	10	11
Patch	3	295	467	133	305	NR	NR
Patch	4	0	138	0	82	0	7
Patch	5	**253**	**113**	**161**	**100**	44	45
Patch	6	**112**	**60**	**118**	**50**	**16**	**12**
Binary	1	**102**	**47**	**55**	**27**	**5**	**1**
Binary	2	**300**	**272**	**211**	**201**	**13**	**9**
Binary	3	**135**	**117**	**109**	**80**	**5**	**2**
Split	1	**442**	**276**	**261**	**166**	**20**	**6**
Split	2	**112**	**22**	**71**	**18**	**5**	**2**
Split	3	**25**	**16**	**18**	**11**	**3**	**0**

n = 12) for visits to flowers, and 0.046 ($Z = 1.69$, n = 11) for number of bees (one-tailed Wilcoxon matched-pairs tests). Nectar volumes in clipped inflorescences did not differ significantly from nectar volumes in control inflorescences (Mann–Whitney U-test, $p = 0.32$), suggesting that the clipping treatment did not inhibit nectar production. Bees preferred the "clipped control" inflorescences over manipulated inflorescences in replicate no. 1. This suggests that the injury inflicted on the plants by clipping did not, by itself, repel pollinators.

L. stoechas

The prevalence of bracts, and bract-flower synchrony

70.4% of 281 blooming inflorescences sampled on three dates bore bracts. Eleven out of 99 inflorescences followed throughout the blooming season did not develop any bract. In the remaining inflorescences, bracts were maintained for 33.58 ± 13.91 d (mean ± SD), while flowering lasted 46.56 ± 6.34 d. Bracts appeared 4.83 ± 3.72 d before the onset of flowering, and wilted 18.05 ± 13.91 d before flowering ended. Flowers and bracts overlapped for 27.59 ± 11.73 d, that is, during 59.59 ± 25.88% of the duration of blooming. Taking into account the fact that bracts were totally absent in 11% of the inflorescences (i.e., zero overlap between bracts and flowers), the probability that a blooming inflorescence would carry a bract was 0.54. The probability that a bract would signal a blooming inflorescence was 0.86.

Bract size and the number of open flowers

The blooming period of our study population extended from early January to early May, and peaked between mid-March and mid-April. The blooming span of individual shrubs was 90.83 ± 17.19 d (mean ± SD, n = 30). We constructed a blooming diagram for each of the sixty inflorescences surveyed during this period. Blooming occurred in each inflorescence in 3–4 waves. The number of open flowers typically peaked four days after the onset of blooming. The second and third peaks occurred after 12–18 and 25–35 days, respectively. The fourth peak, which was much less pronounced (and at times missing altogether) occurred at least 40 days after the onset of flowering. Bracts were usually present in the inflorescence during the first 1–2 blooming peaks, but not during the third and fourth peaks. Bract cluster size remained unchanged during the whole display period.

Bract manipulation experiments

Pollinators landed on intact inflorescences more frequently than on bractless inflorescences in 9 out of 14 observations. This frequency does not significantly differ from 0.5 (sign test, n = 14, $p = 0.212$). The number of visits to intact inflorescences was higher than to clipped inflorescences in 11 out of 17 observations. This preference is not statistically significant either (sign test, n = 17, $p = 0.166$). The mean numbers of pollinator arrivals and flower visits were not significantly affected by bract cluster removal (Wilcoxon matched-pairs tests, n = 14, $Z = 1.04$, $p = 0.30$ for number of arrivals, n = 17, $Z = 0.87$, $p = 0.38$ for number of visits).

DISCUSSION

The main manipulation in the present study involved the removal of flag-like bracts from the inflorescences of two plant species of the mint family. Following the manipulation, honeybees made fewer visits to *S. viridis* plants that lacked flag-like bracts than to control plants. This result supports the hypothesis that terminal clusters of colored bracts function as advertising organs that attract pollinators. In this experiment, we did not control for the possible memorizing of bract locations by pollinators. Thus, some of the bees' visits to clipped inflorescences may reflect their memory of patches that had borne bracts in the past. A similar reduction in pollinator visits was obtained by petal removal from flowers in plant species that lack bracts (Bell, 1985; Kudoh and Whigham, 1998). We obtained different results in *L. stoechas*: honeybees did not significantly prefer control inflorescences over clipped ones. This finding concurs with similar previous manipulations on *L. stoechas* (Devesa et al., 1985; Herrera, 1997), but conflicts with the hypothesis that pollinators prefer flagged inflorscences (Faegri and van der Pijl, 1979; Barth, 1985; Gottsberger and Hartmann, 1988; Proctor et al., 1996)

The two study species also differed in the correlation between bract display and food reward, i.e., in the reliability of bracts as advertising cues. Bracts provide more reliable signals of food rewards in *S. viridis* than in *L. stoechas* in two respects: (a) In *S. viridis*, bracts may provide false-positive signals of reward (i.e., bracts exist in the absence of open flowers), but false-negative signals (open flowers with no bracts) are very rare. In *L. stoechas*, bracts are frequently associated with both false-positive and false-negative signals. (b) In *S. viridis*, various measures of display size (number of flag-like bract clusters, number of leaves per bract cluster, bract cluster length) are consistently and positively correlated with reward parameters. This is not the case in *L. stoechas*, where the number of open flowers, but not bract cluster size, fluctuated in each inflorescence during the blooming season.

Our data thus show that *Salvia* bracts are both more effective and more reliable display cues than *Lavandula* bracts as signals that indicate nectar rewards in the inflorescences below them. It is tempting to suggest a

cause-and-effect relationship between the reliability and the effectiveness of the flag-like displays: pollinators may learn to orient to *Salvia* bracts, but may also learn to disregard *Lavandula* bracts as dishonest advertising signals. Alternatively, *S. viridis* bracts may be more attractive to pollinators because they provide a larger visual stimulus, relative to the inflorescence. *S. viridis* bract signals may exert a larger effect on pollinators' patch choices because they are detectable from a greater distance (Vaknin et al., 1996). Pollinators learn display cues mainly on their way to the food source. This learning requires an exposure of at least 3 s of the display stimulus (Menzel, 1985). As detection distance increases, the pollinator spends more time en route, allowing more time for learning the display cue. This mechanism suggests that large bracts (as in *S. viridis*) may affect pollinator choices more strongly than smaller bracts (as in *L. stoechas*).

Our results do not point to any evolutionary advantage to the asynchronous development of flag-like bracts and flowers in *L. stoechas*. Unlike other cases of deception in plant–pollinator systems (e.g., deceptive orchids, Dafni, 1984), no pollination benefit is expected for plants that attract pollinators by carrying flag-like bracts, but do not bloom. Moreover, the maintenance of bracts before blooming may reduce the total amount of resources available for reproduction, and may therefore be maladaptive. A possible interpretation is that the asynchrony between bracts and flowers reflects a developmental, non-adaptive constraint (Herrera, 2001): from a pollination point of view, flag-like inflorescences can be viewed as equivalent to flowers because they contain display, reward, and sex structures. Unlike flowers, however, the display structure is situated at a distance from the sex and reward organs and is related to the whole inflorescence, rather than to a single flower. This feature may pose a constraint on synchronized development of flowers and displays. Indeed, bract displays remain conspicuous in several species (e.g., *Salvia sclarea, Bouganvillea* spp.) long after the flowers associated with them have finished blooming. Constraints on the synchronized development of bracts and flowers are likely to limit the selective advantage of flag-like bracts. This may explain why flag-like bracts are such a rare phenomenon in plants: out of ca. 4500 genera in the Mediterranean flora, only four genera possess species with flag-like bracts: *Muscari*, *Leopoldia*, *Lavandula,* and *Salvia*. While the flag-like displays of *Salvia* and *Lavandula* are composed of bract clusters, the displays of *Muscari* and *Leopoldia* are formed by aborted, transformed flowers. Regardless of their morphological origin, the displays are colored and much more conspicuous than the flowers.

An alternative explanation for the asynchrony of flowers and flag-like bracts is that bracts have evolved for a function other than pollinator attraction, such as defense from radiation damage, drought, or herbivory (Galen and Cuba, 2001; Armbruster, 2002). According to this hypothesis, the presence of anthocyanins in vegetative organs, such as bracts, is selected for reasons unrelated to pollination. If the main function of bracts is indeed chemical defense from herbivores, then they should be selected to appear during the period of maximal grazing pressure. Such selection could decouple bract development from flowering if the time of maximal herbivory does not coincide with blooming (but see Herrera, 1993, for temporal patterns of herbivory on *L. stoechas*).

Table 5

Observations of bee and fly behavior on inflorescences with flag-like bracts. One hundred pollinator visitation sequences were observed for each plant species. For each visitation sequence, we noted the type of pollinator (fly or anthophorid bee), and whether it included the flag-like bracts, the flowers, or both

Plant species	Inflorescences observed	Pollinator type	No. of visitation sequences to		
			Flag-like bracts only	Flowers only	Flowers and bracts
Leopoldia comosa	2	Flies	12	1	3
		Anthophorid bees	0	81	3
Salvia viridis	1	Flies	5	1	0
		Anthophorid bees	0	94	0
Muscari commutatum	3	Flies	33	1	15
		Anthophorid bees	0	48	2
Eremurus spectabilis	1	Flies	4	0	1
		Anthophorid bees	0	95	0

The similarity in pollinator visitation rates to bract-bearing and bractless inflorescences of *L. stoechas* begs the question whether any pollination-related selective pressures favor bract development in this species. The following selective advantages have been proposed: (a) Flag-like bracts may increase *L. stoechas* detectability to pollinators mainly in low-density, established populations (Herrera, 1997); (b) Flag-like bracts convey information on the location of *L. stoechas* shrubs mainly to young naïve foragers on their very first flights. As these pollinators gain experience, they learn other cues associated with the plants, such as their location (Wehner and Menzel, 1990), reducing their reliance on the bract display; (c) Flag-like bracts may attract pollinators from long distances to the general area of the flowering patch, but insects' choice of specific inflorescences at short distances is guided by different cues. In other words, bracts may function as "detective cues" that advertise a plant's location rather than as "selective cues" that advertise its quality (Lewis and Lipani, 1990; Cohen and Shmida, 1993); (d) Flag-like bracts may provide plants with a mechanism to discriminate between potential pollinators and to evade the less efficient ones (Proctor et al., 1996). Preliminary observations in four species of plants with flag-like bracts indicate that flies direct a higher proportion of their flights to bracts (rather than flowers) as compared to bees (Table 5). Similarly, removal of bracts from *Mussaenda frondosa* inflorescences reduced pollination visits by butterflies, but not by bees and birds (Borges et al., 2003). Bees are considered more efficient pollinators than flies and butterflies since they fly longer distances and are more flower-constant (Waser, 1983). The presence of flag-like bracts may thus increase the probability of pollination by bees (Menzel and Shmida, 1993). We were not able to compare bee vs. fly attraction to bracts in the present study, as almost all observed pollinators were honeybees. We suggest that this issue deserves further study in field sites that contain several pollinator groups.

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