

POLLINATION ECOLOGY AND THE SIGNIFICANCE OF FLORAL COLOR CHANGE IN *LUPINUS PILOSUS* L. (FABACEAE)

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ABSTRACT

Floral color change was studied in *Lupinus pilosus* L. to elucidate its ecological significance for both the plant and the pollinators. It was found that the change in the banner spot from white to purple was enhanced by artificial pollination. White phase flowers offered more pollen as reward to foraging pollinators than did purple phase flowers. The changes in color and reward were recognized by the pollinators and affected their foraging behavior. Pollinators preferred pre-change flowers and avoided post-change ones, thus increasing the chance that white phase flowers would be pollinated. It is suggested that the increase in outcrossing rate caused by pollinator activity could be the advantage and the driving force for the evolution of the color change mechanism in *L. pilosus*.

INTRODUCTION

In most plant species flower parts unrelated to fruit development wither or drop after the stigmas become nonreceptive or following fertilization (Gori, 1983). Other species retain their flowers well beyond this stage. Retention of old flowers may enhance the attractiveness of the plant to pollinators (Gori, 1983, 1989; Cruzan et al., 1988; Weiss, 1991), or may not (Casper and La Pine, 1984). Retention of old flowers may also be the result of physiological constraint when senescence or abscission of attractive structures cannot happen quickly (Delph and Lively, 1989). In many such species either general or local floral color changes occur (Weiss, 1991).

Floral color change is taxonomically and geographically widespread, occurring in at least 214 genera and 74 families — 21% of the angiosperm families (Weiss, 1991). Pre-change flowers contain more nectar or pollen rewards than do post-change flowers, and are receptive and have viable pollen in contrast with post-change ones (Casper and La Pine, 1984; Lamont, 1985; Eisikowitch and Rotem, 1987; Lamont and Collins, 1988; Weiss, 1991). Most pollinators, including bees, butterflies, moths, flies, beetles (Lamont, 1985; Weiss, 1991), and birds (Delph and Lively, 1985; Lamont and Collins, 1988) discriminate between floral color phases which influence their movement and behavior. By visiting the reward-rich pre-change flowers, pollinators increase their

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foraging efficiency (Heinrich, 1975). By visiting the same young or unpollinated pre-change flowers they also increase the efficiency of pollen receipt and donation (Schaal and Leverich, 1980; Cruzan et al., 1988; Gori, 1989). As a result, floral color change can benefit both plant and pollinator.

The species *Lupinus pilosus* L. (Fabaceae) (Feinbrun-Dotan and Danin, 1991) (syn. *L. pilosus* Murr.; *L. varius* L. subsp. *orientalis* Zohary, 1972) is an East Mediterranean annual species which grows in the Mediterranean regions of Israel in open fields on a variety of soil types. *Lupinus pilosus* blooms in spring and forms dense blue patches seen from a distance.

Chromosome numbers, breeding system, outcrossing rates, hybridization with other species, flower development, and mechanism have been studied in *L. pilosus* (Pazy et al., 1977, 1981; Plitman et al., 1980; Pazy, 1982, 1984; Horovitz and Harding, 1983; Alon, 1986). Some research has been done on the pollination ecology of New World lupines but not on those of the Old World (i.e., Schaal and Leverich, 1980; Gori, 1983, 1989; Juncosa and Webster, 1989; Stead and Reid, 1990; Karoly, 1992).

L. pilosus flowers are arranged in racemes made up of whorls formed by five flowers each. All flowers within a whorl open on the same day, with whorls maturing acropetally. The flowers are blue with white banner spots on the standard petal at the beginning of anthesis, the banner spot turning pink and later purple. The flower has two types of stamens: antisepalous stamens with large elongated (4 mm) anthers and antipetalous stamens with small (1 mm) round ones. Before anthesis anthers dehisce introrsely, and thereafter the pistil and filaments of the antipetalous stamens elongate rapidly, forcing the mass of pollen into the acumen of the keel petals (Alon, 1986). Pollen is viable and the stigma is receptive throughout the flowering time (Alon, 1986). Bees visiting the flower depress the wing and keel petals and as a result some pollen is squeezed out and gathered by the bees. *L. pilosus* is self-compatible and facultatively autogamous with self-pollination occurring spontaneously, but enhanced by natural or artificial triggering of the flower (Pazy et al., 1981; Pazy, 1984; Alon, 1986).

The aim of the present research was to study the ecological significance, both for the plant and the pollinator, of floral color change in *Lupinus pilosus* L. Specifically, the study addresses the following questions:

1. Is floral color change affected by pollination?
2. Do pre-change flowers with white banner spot offer more pollen to pollinators than do purple flowers?
3. Are pre-change flowers preferred by the pollinators?
4. Is fruit set affected by pollination and by the position of the flower within the inflorescence?

MATERIALS AND METHODS

STUDY AREA

The study was carried out in spring 1991 with supplemental observations in spring 1993, at Mt. Carmel, Israel (35°04'E, 32°38'N).

FLORAL COLOR CHANGE AND FRUIT SET

Twenty plants were randomly chosen, in a 1000 m² homogeneous patch, and bagged in fine nylon mesh that prevented visitation of insect pollinators. Ten plants served as unpollinated controls and ten were artificially cross-pollinated on their first day of anthesis. Cross-pollinated flowers were not emasculated because there is no way to do it without damaging the flowers. The flowers were marked and the duration of each color phase was recorded daily for each flower in the first most basal and in the second whorls in each of the control and treated plants. A total of 40 flowers were observed. Fruit set was recorded for each flower.

FLOWER MORPHOLOGY AND POLLEN REWARD

Fresh flowers were collected in the field and brought to the laboratory for morphological measurements and pollen weighing. The length of the style and both types of stamens were measured in 10 flowers in the various color phases during anthesis in untreated flowers. The amount of pollen released by a single triggering of 10 flowers in each color phase was weighed, as was the total amount of pollen per flower. Weighing was done with a Sartorius 2001 MP2 analytical balance.

FORAGING BEHAVIOR

The foraging behavior of *Apis mellifera* and *Anthophora* sp. was observed in three sites at three dates for about an hour each time. A total of 877 visits of bees to flowers were observed, while counting the flowers of each banner spot color phase visited by each bee. Foraging times of 83 honey bee visits to flowers of all the three color phases were measured. On each observation day, the number of flowers of each color phase at the observation site was counted, and the proportion of each phase was calculated.

DATA ANALYSIS

Two-way ANOVA was used to test the influence of the position of the flower, either in the first basal or in the second whorl, and the influence of artificial pollination on the duration of the various color phases of the banner spot and on fruit set. Whenever the model was found to be significant ($p < 0.05$), one-way ANOVA with posteriori Duncan's multiple range test was used in order to compare the effects of flower position and artificial pollination on fruit set and duration of color phases.

Chi-square test was used to test the hypothesis of random visits of the bees among different color stages.

Statistical analyses were carried out by SAS PC (SAS, 1985).

RESULTS

FLOWER DEVELOPMENT

L. pilosus flowers had a mean longevity of 7.1 ± 0.8 days ($n = 40$), which varied according to treatments and flower position. The antisepalous stamens and style elongated simultaneously with aging, allowing the ejection of pollen as a result of flower triggering. The stigma was surrounded by a collar of short unicellular epidermal hairs

Table 1

Mean flower age (0 = onset of anthesis), color of banner spot (BS), mean length \pm S.D. of style, of antipetalous (AP), and of antisepalous (AS) stamens in each developmental stage in *Lupinus pilosus* flowers

Developmental stage	Flower age (days)	Style length (mm)	AP stamens (mm)	AS stamens (mm)
Flower buds	-1-0	18 \pm 0.9	18 \pm 0.7	14 \pm 0.7
Flowers with white BS	0-3	19 \pm 0.9	18 \pm 0.8	19 \pm 0.9
Flowers with pink BS	3-4.5	20 \pm 1.1	18 \pm 0.8	20 \pm 1.0
Flowers with purple BS	4.5-7.5	21 \pm 1.0	18 \pm 0.7	20 \pm 1.0
Wilted flowers purple BS	>7.5	21 \pm 1.2	18 \pm 0.9	20 \pm 1.2

which, one day before anthesis, covered no more than 25% of the stigma and did not elongate further (Table 1).

The amount of pollen released by a single triggering (Fig. 1) was significantly different in different banner spot color phases of open growing flowers (one-way ANOVA, $n = 30$, $F_{2,27} = 76.12$, $p < 0.0001$, $R = 0.849$). The total amount of pollen in the same flowers (Fig. 1) was also significantly different in flowers of different banner spot color phases ($n = 30$, $F_{2,27} = 90.00$, $p = 0.0001$, $R = 0.869$).

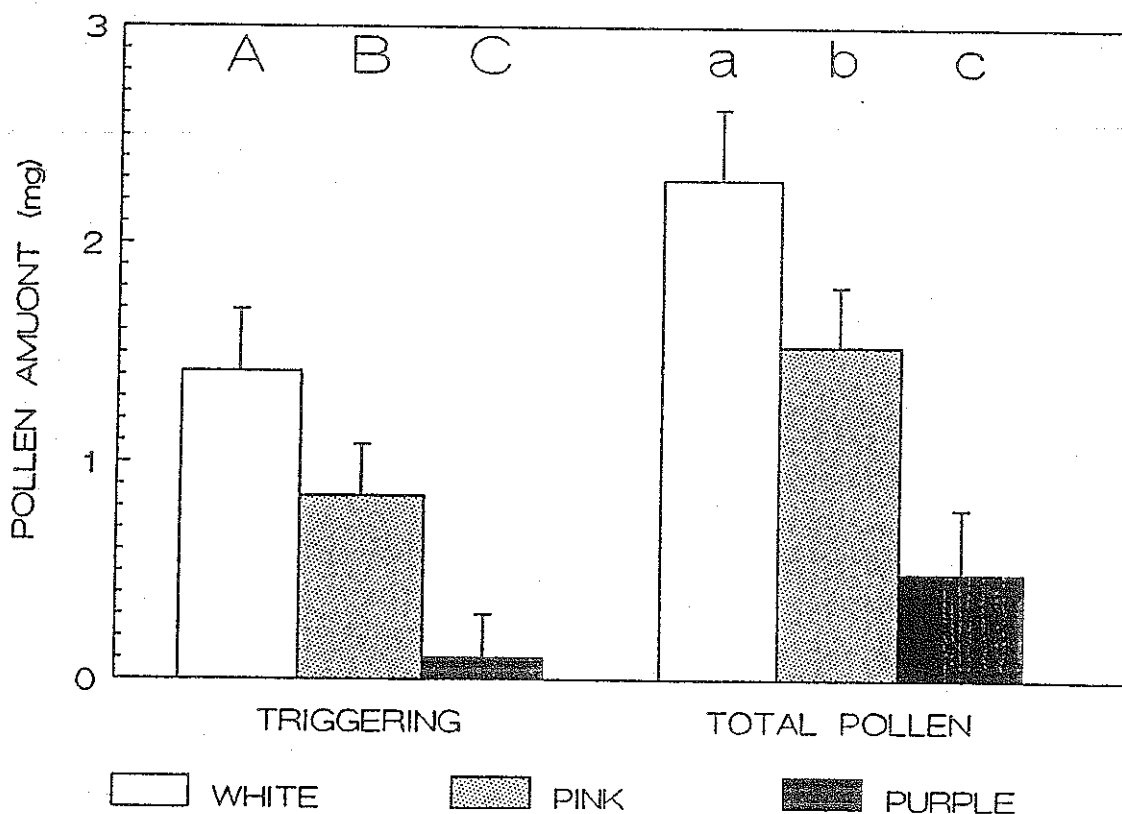


Fig. 1. The weight (mg) of pollen released by a triggered flower and the total weight of pollen in an open untreated flower in each banner spot color phase. Vertical bars represent S.D. Columns with different letters are significantly different as tested by Duncan's multiple range test ($p < 0.05$).

THE EFFECT OF POLLINATION ON COLOR CHANGE AND FRUIT SET

Both artificial pollination and position had a significant effect on color change and fruit set, but the interaction between the two had no effect (Table 2). The white phase was shorter in the second whorl and was shortened by pollination in both whorls (Fig. 2), and thus enhanced color change. There was no significant effect of artificial pollination or of flower position on the duration of the pink banner spot color phase. Only pollination had a significant effect on the duration of the purple banner spot color phase, which was longer in the second whorl of pollinated flowers. Both pollination and position had significant effects on flower longevity. Flower longevity was longer in the first whorl, but shorter in pollinated flowers within it. However, there was no effect of pollination in the second one (Table 2, Fig. 2).

Table 2

Two-way ANOVA results testing the effect of flower position, either in the basal first or second whorl, the effect of pollination, and the interaction of both variables (whorl* pollination) on duration of the various color phases of banner spot, flower longevity, and on fruit set

Variable and source of variation	R^2	df	F	p
A. White BS duration				
Model	0.54	3	14.01	0.0001
Main effects				
Whorl		1	11.69	0.0014
Pollination		1	26.69	0.0001
Whorl* pollination		1	3.37	0.0746
B. Pink BS duration				
Model	0.05	3	0.63	0.5989
Main effects				
Whorl		1	1.46	0.2344
Pollination		1	0.04	0.8360
Whorl* pollination		1	0.39	0.5356
C. Purple BS duration				
Model	0.21	3	3.21	0.0343
Main effects				
Whorl		1	3.50	0.0697
Pollination		1	6.03	0.0190
Whorl* pollination		1	0.11	0.7434
D. Flower longevity				
Model	0.37	3	7.00	0.0008
Main effects				
Whorl		1	14.42	0.0005
Pollination		1	4.73	0.0363
Whorl* pollination		1	1.86	0.1811
E. Fruit set				
Model	0.38	3	14.01	0.0001
Main effects				
Whorl		1	19.92	0.0001
Pollination		1	1.85	0.1828
Whorl* pollination		1	0.04	0.8472

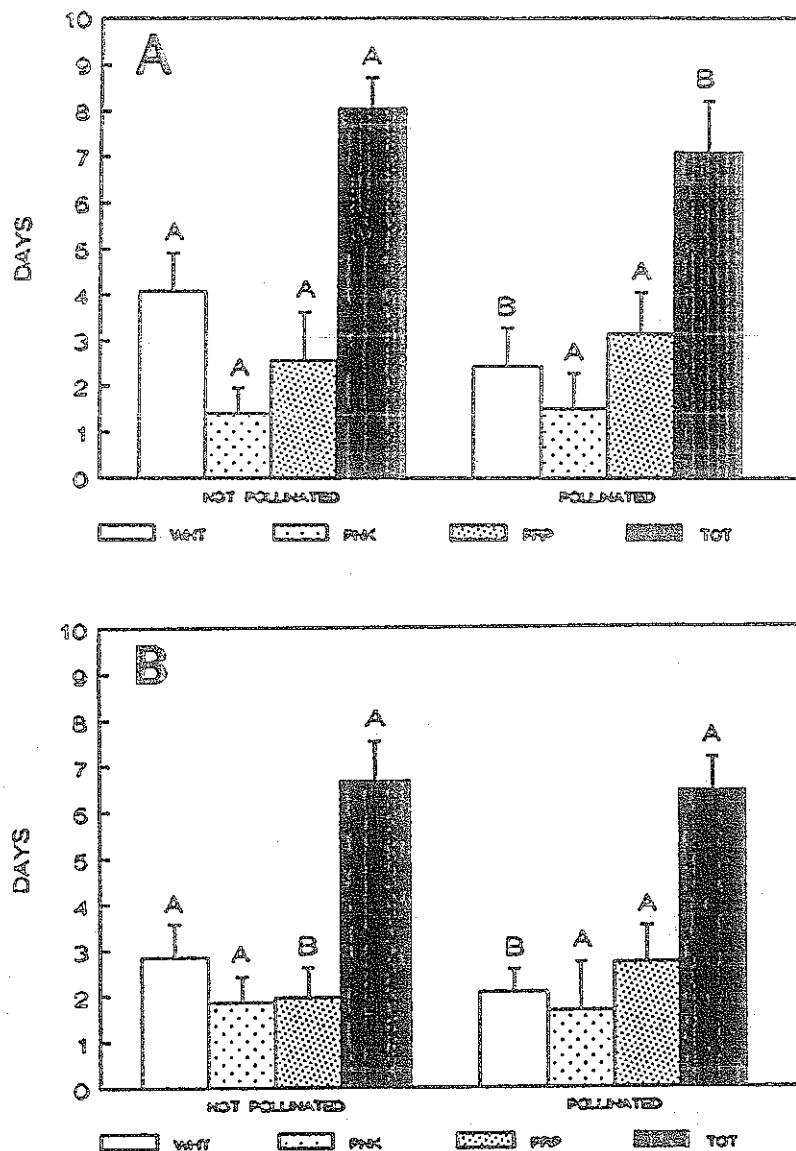


Fig. 2. The effect of artificial pollination on the duration of each banner spot color phase in (A) the first basal whorl of *L. pilosus* flowers, and in (B) the second whorl. WHT white banner spot, PNK pink banner spot, PUR purple banner spot and TOT, flower longevity. Vertical bars represent S.D. Columns with same patterns and different letters within each whorl are significantly different as tested by Duncan's multiple range test ($p < 0.05$).

Flower position had a significant effect on fruit set (Table 2), which was lower in the flowers of the second whorl than in flowers of the first one (Fig. 3). Fruit set in both whorls tended to be higher in artificially cross-pollinated flowers than in untreated ones (Fig. 3), but the differences were not significant (Table 2).

FORAGING BEHAVIOR OF POLLINATORS

Pollen-gathering honey bees and the solitary bee *Anthophora* sp. were the major visitors to the flowers of *L. pilosus*, and they activated the flowers' mechanism that

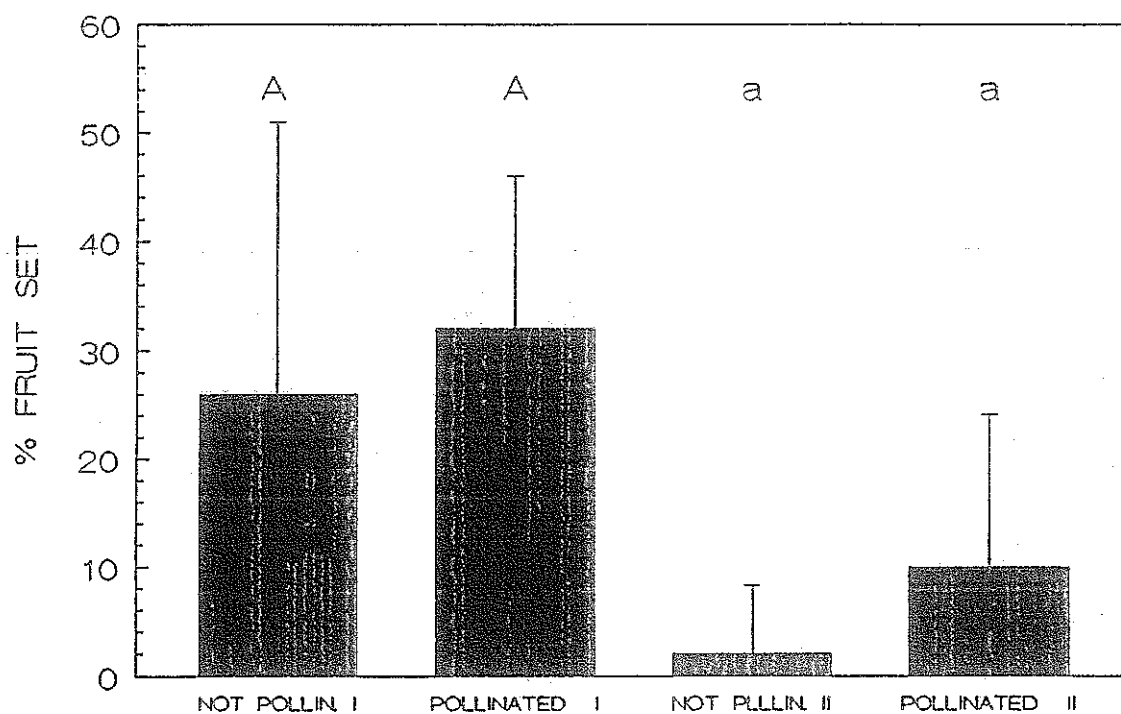


Fig. 3. The effect of artificial cross-pollination, and position of flower on % fruit set. NOT POLLIN. I and NOT POLLIN. II, are not pollinated flowers in the first basal and second whorls, respectively. POLLINATED I and POLLINATED II are pollinated flowers in the first basal and second whorls, respectively. Vertical bars represent S.D. Columns with different letters are significantly different as tested by Duncan's multiple range test ($p < 0.05$).

causes pollination. Small solitary bees and flower beetles were occasionally found visiting flowers, but were incapable of activating the mechanism and thus were not considered as legitimate pollinators. Honey bees and *Anthophora* sp. significantly preferred the white banner spot color phase flowers and avoided the purple ones in all sessions but one (Table 3). The intermediate pink color phase received more visits than expected in some cases and in some less.

The mean time spent by honey bees foraging on flowers of various banner spot color phases was 15.4 ± 15 ($n = 30$), 16.3 ± 16.6 ($n = 34$), and 8.0 ± 5.1 s ($n = 19$) on the white, pink, and purple phases, respectively. In spite of the large difference in the foraging times, it was found to be not significant ($F_{2,80} = 2.26$, $p = 0.1106$). However, when the white and pink flowers were treated as one group, since the foraging time spent on them was almost identical, the mean foraging time was 15.9 ± 16.0 s ($n = 64$) on white/pink flowers, 8.0 ± 5.1 s ($n = 19$) on purple flowers, and the difference was significant ($F_{1,81} = 4.51$, $p < 0.05$).

Table 3

Comparison between the observed (Obs) number of flowers of each banner spot (BS) color phase and the expected (Exp) one (according the relative abundance of each phase in the field). H_0 hypothesis of the χ^2 test for goodness of fit was that there was no difference between the observed and expected number of visits. NS = $p > 0.05$, * = $p < 0.001$

Date	Pollinators		White BS		Pink BS		Purple BS		χ^2	p
			No.	%	No.	%	No.	%		
27.3.91	Honey bees	Exp	35.5	67.0	11.7	22.0	5.8	11.0	4.15	NS
		Site 1	Obs	35	66.0	16	30.0	2		
28.3.91	Honey bees	Exp	23.4	33.0	32.0	45.0	15.6	22.0	31.86	*
		Site 1	Obs	44	62.0	11	16.0	16		
15.3.93	Honey bees	Exp	198.5	63.0	50.4	16.0	66.1	21.0	56.36	*
		Site 2	Obs	249	79.0	60	19.0	6		
15.3.93	Honey bees	Exp	151.0	50.5	49.3	16.5	98.7	33.0	168.80	*
		Site 3	Obs	260	87.0	31	10.5	8		
15.3.93	Anthophora	Exp	87.6	63.0	22.2	16.0	29.2	21.0	43.91	*
		Site 2	Obs	123	79.0	15	19.0	1		

DISCUSSION

COLOR CHANGE

In *L. nanus* color change was not pollination dependent (Juncosa and Webster, 1989), while in some other lupine species (Wainwright, 1978; Schaal and Leverich, 1980; Stead and Reid, 1990), the banner spot color change was influenced by pollination. In *L. pilosus*, both aging and pollination are the causes for floral color change.

The senescence of flowers has been shown to be influenced by pollination (Halevy, 1986; Stead, 1992). Flower color change could be the result of ordinary senescence of the flower at the end of flower viability, or could take place in an earlier phase as a result of pollination (Gori, 1983) or nectar withdrawal (Eisikowitch and Lazar, 1987). Since it is most likely that an old flower will already have been pollinated, both mechanisms causing flower color change are suitable to direct the pollinators to unpollinated flowers. However, it is clear that the maximal impact of flower color change on minimizing visits of pollinators to pollinated flowers is when it takes place as a result of pollination itself.

In *L. albifrons* pollination caused an increase in ethylene production by the keel and pistil, which in turn caused an increase in anthocyanins in the banner spot (Stead and Reid, 1990). Since ethylene has a general effect on flower senescence (Stead and Reid, 1990), it seems that this mechanism can be assumed to be a general one.

REDUCTION OF REWARD

Color by itself is of limited importance to bees (Waser, 1983) unless it is immediately reinforced by stimulation of reward (Waddington, 1983). In many flowers offering nectar, the secretion stops as a post-pollination effect (Lamont, 1985; Eisikowitch and Rotem, 1987; Weiss, 1991). Since all the pollen is produced in the

flower before anthesis, this cannot be the situation in pollen-offering flowers like those of lupines. However, because of foraging activity of pollen-gathering bees, there is a continuous reduction in the amount of pollen during the flowering period in each flower. In *L. pilosus*, as in *L. argenteus* (Gori, 1983), pollinators preferred the pre-change flowers which contained more pollen. The preference for white spotted flowers by bees shows that the age-dependent color-change mechanism is not necessarily inferior to the pollination-dependent one in the regulation of the amount of reward in color-changing flowers.

FLOWER ATTRACTIVENESS AND POLLINATOR ACTIVITY

Retaining old fertilized flowers is an expense of energy and, therefore, it is supposed to confer a reproductive advantage as compensation (Gori, 1983, 1989). Retaining old flowers increased the attractiveness of the inflorescence to pollinators in some of the American lupines (Wainwright, 1978; Schaal and Leverich, 1980), and in other species too (Weiss, 1991). Since *L. pilosus* grows in very dense patches it seems that retaining pollinated and old flowers could increase the attractiveness of both single inflorescences and the patch as a whole, thus increasing the probability that the flowers will be discovered.

Retaining old fertilized flowers increases the total number of flowers and decreases the proportion of the unfertilized flowers on each plant. Thus, in spite of increasing the total attractiveness of the inflorescence it may reduce the chance of pollination for young unfertilized flowers. Color change which directs pollinators to young rewarding flowers and not to old or pollinated ones increases the chance of pollination in the young flowers (Gori, 1983).

L. pilosus flowers, like some New World lupines, were more attractive with a white banner spot (Wainwright, 1978; Schaal and Leverich, 1980; Gori, 1983, 1989; Stead and Reid, 1990), and honey bees spent more time on those flowers, and thus increased the chance of pollination. Thomson and Plowright (1980) found that the amount of pollen on the stigma of a flower was positively correlated with the time the pollinator spent on the flower.

MATING SYSTEM

Many annual lupines are self-compatible (Juncosa and Webster, 1989). *L. pilosus* was found to be a self-compatible autogamous species with low fruit set in spontaneous self-pollinated flowers, and triggering of flowers enhanced self-pollination (Pazy, 1984; Alon, 1986). Artificial cross-pollination had at most a marginal effect on quantity of fruit set (Table 2), indicating a high efficiency of spontaneous self-pollination. Since artificial pollination on the first day of anthesis had an effect on color change, and since the peristigmatic collar was found to be very short, covering only 25% of the stigma, no limitation of self-pollination can be reported for *L. pilosus*. This conclusion agrees with previous reports (Plitman et al., 1980; Pazy et al., 1981; Pazy, 1982, 1984; Alon, 1986). However, in spite of its autogamous nature, an outcrossing rate of 10–60% was reported for *L. pilosus* (Horovitz and Harding, 1983).

LIMITATION AND PATTERN OF FRUIT SET

Fruit set in artificially pollinated flowers was not significantly higher than in unpollinated flowers (Table 2, Figs. 2, 3); thus, it can be stated that spontaneous self-pollination was effective and that cross-pollination was not a limiting factor for fruit set. The results show that fruit set in the basal first whorl was higher than in the second one, and Pazy (1982) found that 80% of the total fruit set in *L. pilosus* was produced in the lower three flower whorls; *L. nanus* was similar (Karoly, 1992). This may be the result of low amounts of stigmatic exudate in the flowers of the upper whorls (Alon, 1986), or shortage of resources (Karoly, 1992). "Extra" flowers could contribute to the overall attractiveness of the inflorescences (Karoly, 1992).

CONCLUSIONS

The present study indicates that flower color change in *L. pilosus* was enhanced by pollination and was accompanied by reduction in the reward offered to foraging pollinators. Those changes were recognized by the pollinators and their foraging behavior was affected by preferring pre-change flowers and avoiding post-change ones. In this study this mechanism did not cause an increase in fruit set, but 30–60% cross-fertilization was found in some populations of *L. pilosus* (Horovitz and Harding, 1983), and only 10% in others (Pazy, 1984). Therefore, it may be suggested that the increase in outcrossing rate caused by pollinator activity (Karoly, 1992) could be the advantage and the driving force for the evolution of color change in *L. pilosus*. Any mechanism that makes pollinator activity more efficient and thus favors outcrossing, even if in low levels, is important in an autogamous plant as it is the only source for genetic variation in the population. It is also possible, however, that color change evolved in an outcrossing relative of *L. pilosus*, and is retained in this autogamous species.

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