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**Floral color change and the attraction of insect pollinators in lungwort (Pulmonaria collina)**

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**Abstract** We studied the effect of floral color change on long- and short-distance attraction of insect pollinators to the herb lungwort, *Pulmonaria collina*. Lungwort flowers change color with age from red to blue. Young red flowers had a significantly greater pollen and nectar reward and were significantly more often unpollinated than old blue ones. Red and blue flowers both influenced long-distance attractiveness of plants, defined as the number of insect approaches towards an individual plant. After reaching a plant, flower visitors preferred to visit young red flowers. Therefore, short-distance attractiveness, defined as the number of flowers visited successively on an individual plant, was influenced mainly by the number of young red flowers. The co-occurrence of the change in reproductive ability, in amount of reward, and in flower color enabled lungwort plants to direct pollinators to reproductive, highly rewarding red flowers. The data suggest that by maintaining changed flowers lungwort plants can increase their long-distance attraction and simultaneously enhance the probability of flower visits to pre-changed flowers. Thus, we propose floral color change as a mechanism that can increase the efficiency of pollen transfer to enhance plant fitness.

**Key words** Flower number · Flower visit · Foraging behavior · Pollen transfer · Pollination

**Introduction**

Floral color change is a common phenomenon among flowering plants (von Linné 1763). There are at least 33 orders, 78 families, and 253 genera of angiosperms with species whose flowers change color (Weiss and Lamont 1997). This wide distribution and the multiple independent evolution cannot be explained by macroecological patterns such as plant life history, habitat use, geographic range, or growth habit (Weiss 1995). Consequently "floral color change has most likely evolved in response to selection by visually orientated pollinators, and reflects a widespread functional convergence within the angiosperms" (Weiss 1995, p. 167). To gain a better understanding of this phenomenon, one has to take into account that changes in floral color are usually accompanied by a decrease in pollen and nectar reward and a loss of male and female reproductive potential of individual flowers (Gori 1983, 1989; Casper and La Pine 1984; Lamont 1985). All these floral characteristics are part of a complex mutualistic system of animal-plant interactions. Floral color change is assumed to benefit both plants and animals (Sprengel 1793; Müller 1883; Delph and Lively 1985; Weiss 1991), but its adaptive nature and ecological significance remain unclear (Fægri and van der Pijl 1976; Faegri and van der Pijl 1976; Fægri and van der Pijl 1976; Fægri and van der Pijl 1976; Fægri and van der Pijl 1976; Fægri and van der Pijl 1976).

We approach floral color change first from a zoological and then from a botanical perspective. In the former case, one has to consider the visual and behavioral characteristics of flower visitors. While foraging, visually orientated animals have to make at least two successive decisions. To increase their foraging efficiency they have to decide first, from longer distances, which plant is most attractive and should be approached. After arriving at the plant, the question arises as to which flower is most attractive and should be visited. Consequently, the approach to a plant and the visit of a single flower have to be distinguished (Knoll 1926; Faegri and van der Pijl 1976; Hess 1983). Assuming possible differences between this long- and short-distance foraging behavior, we correspondingly distinguish between long- and short-distance attractiveness of plants. Plants that are attractive from long distances will receive many approaches of pollinators, while those that are attractive from short distances will receive many successive visits to their flowers. For plants pollinated by visually orientated animals, the total number of open flowers – the size of the floral display – is one of the most im-
important factors influencing the attractiveness at both distance levels (Sih and Baltus 1987; Klinkhamer and de Jong 1993; Harder and Barrett 1995; Robertson and Macnair 1995). In addition, for short-distance attractiveness, the reward offered and found in the flowers by visiting animals plays a major role (Schemske 1980; de Jong et al. 1993; Klinkhamer and de Jong 1993).

When looking at floral color change from a botanical perspective, one has to consider the pollinator activity on plants and the resulting pollen transfer. Plants with larger floral displays increase the number of pollinator approaches due to a strong long-distance attractiveness (Sih and Baltus 1987; Hessing 1988). This affects outcrossing success by enhancing the import of outcross pollen (Klinkhamer and de Jong 1990; Harder and Barrett 1995). However, as a consequence of strong short-distance attractiveness and long visiting bouts to individual plants, large floral displays can cause geitonogamous pollination (de Jong et al. 1992; Klinkhamer et al. 1994; Harder and Barrett 1995; Barrett and Harder 1996). Geitonogamy, transfer of pollen between flowers of the same plant, can be disadvantageous for plants through severe pollen wastage and seed loss (Lloyd 1992) and reduction of male and female fitness (de Jong et al. 1993). Thus, for outcrossing success, plants should attract many pollinators to the plant, but each pollinator should visit only a limited number of flowers successively on an individual plant (Klinkhamer et al. 1994; Iwasa et al. 1995). However, because both long- and short-distance attractiveness increase with flower number, attractiveness to pollinators is a plant’s dilemma (Hessing 1988; Klinkhamer and de Jong 1993).

Working with lungwort of the species *Palinorinia collina* Sauer, we studied floral color change with respect to its possible effects on long- and short-distance attraction of flower visitors. *P. collina* is a herb that simultaneously displays many intensively colored flowers which change color from red to blue with age. Lungwort is pollinated by bees, bumblebees, butterflies, and some butterflies (Knuth 1898; Westrich 1989; Oberrath et al. 1995). We asked three questions: (1) Are flower visitors of *P. collina* physiologically able to distinguish red–from blue-colored flowers? (2) What is the effect of different colored flowers on both long- and short-distance foraging behavior of flower visitors and long- and short-distance attractiveness of plants? (3) Can floral color help the plants improve their long-distance and simultaneously reduce their short-distance attractiveness?

### Methods

**Plant species, location and time of study**

Individual plants of *P. collina* can simultaneously produce up to ten stalks with three to four inflorescences per stalk and two to four simultaneously open flowers per inflorescence. The median of total flower number in the population studied was 14.5 (25–75% quartile: 8.25–25.75, maximum: 87, n=100) with a proportion of red flowers of 58.8±21.6% (mean±SD). The number of red flowers, number of blue flowers and total flower number were all positively correlated. Nectaries are located at the bottom of a corolla tube of nearly 1 cm length, where nectar can accumulate. The number of pollen grains, which are produced by five anthers, exceeds 50,000 per flower. There is no mechanism to expose the pollen grains successively (W. Sauer, personal communication). The pollen grains are exposed when the flower is open. Insects forage for both nectar and pollen (Knoll 1926; Westrich 1989, personal observations). During anthesis, the color of the corolla changes from red through purple to violet and finally blue. Lungwort flowers are hermaphroditic and homogamous (both receptive stigmas and pollen-bearing anthers can be found simultaneously), heterostylos (long- and short-styled flowers can be found), and self-incompatible (Hildebrand 1865; Knuth 1898; Kostka 1922; Dublerger 1992). Flowering time ranges from March to May.

All plants studied belonged to a single population of more than 300 individuals growing in a meadow partly surrounded by forest. Minimum distance from one to the next lungwort plant was less than 1 m for 90% of the individuals (n=96) with an average density of approximately one plant per square meter. The population is found in the Rohrhaldenbachtal, a small valley of the Rammert, a range of hills 8 km southwest of Tübingen, Baden-Württemberg, Germany. We conducted the study from March to May 1995.

Floral colors and their perception by insects

We divided the flower colors of *P. collina* into two categories (hereafter called color phases). We distinguished between young flowers with several shades of red and light violet (hereafter called red) and old flowers with deep-violet or blue coloration (hereafter called blue).

To investigate whether flower visitors of lungwort are able to perceive the color difference between red and blue flowers, we compared the changes in the spectral reflection of *P. collina* petals (Fig. 1b) with the color discrimination function of the insect eye (Fig. 1d). Light reflection functions of petals and blue flowers were measured irradiating the flowers with a 20-W halogen lamp and using an MMS Zeiss Jenoptik diode array spectrometer with 265 diodes, fiber optics, and 14-bit analog-digital-change. The measurements were performed at the Department of Physical Chemistry, University of Tübingen. We measured the reflection spectra of three young red and three old blue flowers between 390 and 706 nm in steps of approximately 3.3 nm. For each measured wavelength, we calculated the mean reflection (Fig. 1a) and divided the mean values of blue flowers by these of red ones. We used this quotient as an index for color change (Fig. 1b). For the color discrimination of the insect eye, we present the data of the main lungwort flower visitor, the bee *Anthophora acervorum* (Fig. 1c,d). These data were taken from Peitsch et al. (1992) in which data for several species of flower visitors are available. In this study, the color discrimination function (Fig. 1d) is derived from the spectral sensitivities of the photoreceptors (Fig. 1c) by application of two color discrimination models, the just-noticeable differences in photoreceptors (model I in Fig. 1d) and the neuronal coding in spectral antagonistic neural systems (model II in Fig. 1d). For more information see Peitsch et al. (1992).

To document the temporal pattern of color change under natural conditions, we marked 53 flowers on 38 individual plants in the field shortly before bud opening. We determined the color category of each flower every day until the corolla faded or fell off. For plants with more than one investigated flower, we calculated average values.

**Amount of reward**

The primary attractants of lungwort are nectar and pollen. To quantify the amount of reward offered by different-colored flowers, we quantified the amount of nectar and pollen. Before measuring the quantity of nectar, we bagged the whole plant for 4–5 h to ensure nectar accumulation. We sucked up the nectar with glass capillaries scaled in microliters. We determined the quantity of nectar of 375 flowers on 50 randomly chosen plants. For each

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Fig. 1 Light reflection curves of lungwort flowers (a,b) and color perception function of Anthophora acervorum (c,d after Peitsch et al. 1992). a Reflection functions of different-colored petals. b Difference in reflection between colors calculated as the quotient of the blue and red reflection function shown in a. c Spectral sensitivity functions of photoreceptors of A. acervorum. d Two-color discrimination functions of A. acervorum derived from spectral sensitivity functions shown in c and based on two different models: model I, just-noticeable differences in photoreceptors, model II, neuronal coding in the spectral antagonistic neural system. The ability to discriminate colors arises from overlaps of the spectral sensitivity function of the three photoreceptors. Such overlaps occurred in A. acervorum around 400 and 500 nm (e). As a result, color discrimination for A. acervorum peaked for both applied calculation models around these wavelengths (d). The reflection of red and blue petals differed distinctly between 480 and 520 nm (a), yielding a corresponding peak in the reflection difference (b). Due to the match between the maximum color difference (b) and the second peak of the color discrimination functions calculated with both models (d), we assume that the main pollinator of lungwort, A. acervorum, was able to perceive the color difference of red and blue flowers.

Observations

Foraging behavior of insects/attraction of pollinators

We watched flower visitors on individual lungwort plants under natural conditions for 102 periods of 20 min each. Each observation period was conducted with plants varying in the size of their floral displays and percentage of red and blue flowers. For each observation period, we counted the number of insect approaches as the approach rate and noted the species of insect. For each approach within an observation period, we counted the number of successively visited flowers. From these data, we calculated for each observation period, the average number of visited flowers per approach as the visitation rate. Data were excluded from analysis if we recognized that an individual insect which had just left the plant returned to the plant observed. For each observation period, we counted the number of red and blue flowers on the plant under observation. To test the effect of neighboring plants on the approach rate, we determined the minimum distance to the next plant and the number of plants within a 1-m radius as measures of plant density. We performed regression analyses to test the effect of flower number and plant density on the approach and visitation rate.

Color choice behavior of insects

We also studied whether the insects preferred to visit red or blue flowers. We determined the color phase of each flower visited. For analysis, we used from each visiting bout the first visit as the insect's color choice because successive color choices within a sequence of visits might not be independent. We compared the observed frequency of visits to red and blue flowers with those expected if animals showed no color preference. Assuming random choice, the expected frequencies were calculated from the number of red and blue flowers counted on the plants.
Experimental manipulation of floral displays

Additionally, we studied color effects on approach and visitation rates in experimentally manipulated plants, with observations made as for naturally flowering plants. We investigated plants with only red and only blue flowers. Plant displays were manipulated such that we obtained 14 pairs of plants. Within each pair, the plants had the same number of flowers, but differed in flower color: one individual had only red, the other only blue flowers. To minimize the problem of time-dependent changes in pollinator activity, we observed the plants of each pair either simultaneously or alternately in periods of 10 min.

Results

Visual perception by insects

and timing of floral color change

To test whether the flower visitors have the physiological ability to perceive the color difference between red and blue lungwort flowers, we compared the light reflection curves of petals of lungwort flowers with the spectral color discrimination function of one of the most common visitors, the bee A. acervorum. The red and blue flower color differed distinctively between 480 and 550 nm (Fig. 1a,b). A. acervorum had, for both of the applied calculation models, its second peak in color discrimination between 480 and 520 nm (Fig. 1d). Other hymenopterans have similar visual characteristics (see Peitsch et al. 1992). Due to the match between the difference in the light reflection curves of lungwort petals (Fig. 1b) and the color discrimination functions of insect pollinators (Fig. 1d), we conclude that the flower visitors should be able to perceive the color difference between the two color phases.

The flowers remained 4.6±1.6 days (mean±SD unless noted otherwise; n=38) in the red phase and an additional 2.0±1.7 days (n=38) in the blue phase. Total flower longevity was 5.8±1.4 days (n=38). The color change took place after approximately 4/5 of the flower total life span.

Rewards of flowers

Red and blue flowers differed significantly in their quantity of nectar (Fig. 2). Young red flowers contained much more nectar than old blue ones (median-test: \(\chi^2=51.3, df=1, P<0.001\)). We found the same pattern for the amount of pollen (Fig. 3). Young red flowers offered more pollen than old blue ones (\(\chi^2=47.2, df=4, P<0.001\)).

Residual reproductive ability

Residual male and female reproductive potential of individual flowers differed between the two color phases. Red flowers had a significantly higher pollen content than blue ones (Fig. 3). The large pollen reward offered by young red flowers implies a higher residual male reproductive ability. In addition, red flowers were significantly more often unpollinated than blue ones. Of the 67 investigated red flowers, we found 31 (46%) already pollinated and 36 (54%) unpollinated. In contrast, of the 68 investigated blue flowers, only 8 (12%) were still unpollinated and 60 (88%) pollinated. This difference was significant (\(\chi^2\)-test: \(\chi^2=28.7, df=1, P<0.001\)). The frequent lack of pollination in red flowers indicates their relatively higher residual female reproductive ability.

Foraging behavior of flower visitors

and attractiveness of plants

Flower visitors

On P. collina plants, we observed in total 21 different insect species from four hymenopteran, two dipteran, and three lepidopteran families. The main flower visitors were the bee A. acervorum (36% of approaches, 24% of visits), the bumblebee Bombus pascuorum (16% of approaches, 20% of visits), and the beeflies Bombylius major (27% of approaches, 34% of visits) and Bombylius discolor (7% of approaches, 11% of visits). Because
Di-sciision

Learning the floral color cue requires repeated visits, we used only the data of these main flower visitors for analyzing short-distance effects (see below).

Long-distance effects

From long distances, red and blue flowers had the same effect on the foraging behavior of insects. To test how the flower color affected the long-distance attractiveness of plants, we performed regression analyses to explain the visitation rate by the number of different-colored flowers. We pooled the data of naturally flowering and manipulated plants to increase the variability in flower number. While red and blue flowers explained the number of insect approaches to a similar extent, total flower number had the significantly strongest effect on the approach rate (Table 1). Therefore, total flower number was the best measure for the long-distance attraction of plants. Old blue flowers had already fulfilled most of their reproductive task. Because the approach rate increased with equal numbers of either red or blue flowers, the red-flowering ones received significantly more visits than blue flowering ones of equal size (paired t-test: t=3.36, df=12, P=0.003; Fig. 4b). Again, red flowers had a clearly stronger effect on short-distance attraction to insects than blue ones.

Correspondingly, flower visitors preferred to visit red flowers. While expecting 146.4 visits to red flowers we observed 186 and while expecting 83.6 visits to blue flowers we observed 44. This difference was significant (χ² goodness-of-fit test: χ²=12.8, df=1, p<0.001).

Short-distance effects

At short distances, the effects of red and blue colors differed significantly. To test how flower color affected the short-distance attractiveness of plants, we performed regression analyses to explain the visitation rate by the number of different-colored flowers. While total flower number and the number of red flowers explained the number of successive visits to a similar extent, blue flowers did not have a significant effect on the visitation rate (Table 2). When comparing the manipulated plants with equal numbers of either red and blue flowers, the red-flowering ones received significantly more visits than blue flowering ones of equal size (paired t-test: t=3.36, df=12, P=0.003; Fig. 4b). Again, red flowers had a clearly stronger effect on short-distance attraction to insects than blue ones.

Discussion

This study yielded two major results. First, in P. collina the effects of red and blue flowers on insect foraging behavior differed clearly at the long- and short-distance level. From longer distances, red and blue flowers had the same positive effect on the number of insect approaches towards individual plants (approach rate). At short distances, however, young red flowers had a stronger influence on the number of successive visits per approach (visitation rate) than old, blue ones. Second, differently aged lungwort flowers not only differed in color but also in their amounts of reward and in their residual reproductive ability.

By retaining flowers beyond their reproductive period, lungwort plants increased their total flower number and raised their long-distance attractiveness. Old blue flowers were more often already pollinated than young red ones and contained little pollen in their anthers. Thus, old blue flowers had already fulfilled most of their reproductive task. Because the approach rate increased

### Table 1 Linear regression analyses of the effect of flower number on the approach rate (n=130 observation periods). Red and blue flowers increased the long-distance attractiveness of plants to a similar extent (difference n.s.). Total flower number was the best measure of long-distance attraction (P<0.05 for comparisons with both red and blue flowers). For analysis, both flower number and approach rate were log-transformed. We tested differences between regression coefficients following Sachs (1992, pp. 553–554) approach rate were log-transformed. We tested differences between regression coefficients following Sachs (1992, pp. 553–554).

<table>
<thead>
<tr>
<th>Variable</th>
<th>b</th>
<th>t</th>
<th>P</th>
<th>Explained variance (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total flower number</td>
<td>0.47</td>
<td>4.5</td>
<td>&lt;0.0001</td>
<td>13.7</td>
</tr>
<tr>
<td>Number of red flowers</td>
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<td>2.0</td>
<td>0.05</td>
<td>2.9</td>
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<tr>
<td>Number of blue flowers</td>
<td>0.18</td>
<td>2.4</td>
<td>0.02</td>
<td>4.3</td>
</tr>
</tbody>
</table>

### Table 2 Linear regression analyses of the effect of flower number on the visitation rate (n=87 observation periods with at least one approach). Red flowers had the greatest impact on the short-distance attraction of plants. While red flowers induced insects to visit flowers, blue flowers did not have a significant effect on the number of successive visits per approach. For statistical methods see legend to Table 1 (total flower number vs red-flower number: n.s.; total flower number vs blue-flower number: P<0.01; red- vs blue-flower number: P<0.01).

<table>
<thead>
<tr>
<th>Variable</th>
<th>b</th>
<th>t</th>
<th>P</th>
<th>Explained variance (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total flower number</td>
<td>0.32</td>
<td>3.0</td>
<td>0.004</td>
<td>9.6</td>
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<tr>
<td>Number of red flowers</td>
<td>0.24</td>
<td>4.0</td>
<td>&lt;0.0001</td>
<td>15.8</td>
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<tr>
<td>Number of blue flowers</td>
<td>-0.02</td>
<td>-0.3</td>
<td>&gt;0.7</td>
<td>0.1</td>
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</tbody>
</table>
with both the number of red and blue flowers, the retention of old, post-changed flowers contributed to the overall showiness and attractiveness to insects. Many authors have suggested this ecological function of retaining changed flowers (Müller 1877; Kugler 1936; Vogel 1950; Schemske 1980; Lamont and Collins 1988; Ne’eman and Nesher 1995), but evidence is rare (Gori 1989; Weiss 1991).

In contrast to the phase of approaching from long distances, insects used mainly the red flower color for orientation on the plant, i.e., at short distances. They preferred to visit young, red flowers whose number determined the length of visiting bouts. Old, blue flowers were avoided and their presence did not induce insects to visit flowers.

These findings fit well with the results of other studies. In studies discriminating between approaches and visits, flower number increased both approach and visitation rate (Schemske 1980; Schmitt 1983; Klinkhamer and de Jong 1990, 1993). Gori (1989) found that after removing old, post-changed flowers, significantly fewer pollinators approached Lupinus argenteus plants, but the number of flowers visited per inflorescence and the number of inflorescences visited per plant remained similar. Kelt (1997) found in Errazurizia megacarpa that equally sized plants of different colored flowers received roughly equal numbers of approaches but unequal numbers of visits.

Insects most likely differentiated young and old flowers by their color. We were able to show that floral color change in P. collina took place at wavelengths around 515 nm. The bee A. acervorum and several bumblebees have a peak of color discrimination ability in the same spectral region (Peitsch et al. 1992). We therefore conclude that these insects were able to distinguish the two floral colors of P. collina. Generally, insect color vision and flower colors show good agreements (Chittka and Menzel 1992). Alternatively, insects might discriminate flowers by their odor. In some plant species, flower odor changes with their color (Casper and La Pine 1984; Lamont and Collins 1988). However, for hymenopterans and bees, visual orientation appears to dominate (Andreae 1903; Knoll 1926; Kugler 1942, 1943; Hess 1983; Westrich 1989) and olfaction seems to play a role only in very close proximity to an individual flower (von Frisch 1965; Fægri and van der Pijl 1976; Barth 1982; Hess 1983; Lunau 1992).

Insects, obviously favored red flowers due to their large quantity of rewards. Hymenopterans and bees forage on both pollen and nectar (Knoll 1926; Westrich 1989; personal observations). Floral color change was correlated with a decline in the amount of pollen and nectar. Naturally, the amount of pollen in flowers decreased with each visit. Due to the color choice of the insects, this happened mainly during the red phase. As a result, pollen was rare in old, blue flowers. In contrast to the amount of pollen, flowers can control their quantity of nectar directly through its production rate. While young red flowers produced large quantities of nectar, old blue flowers produced, at most, little. It is well known that flower-visiting insects are able to learn color cues in order to increase their foraging efficiency (von Frisch 1915; Menzel and Erber 1978; Menzel 1985; Dukas and Real 1991, 1993a, 1993b; Greggers and Menzel 1993; Weiss 1997).

Why did the insects use the color cue only for orientation on the plant and not earlier while approaching the plant? Most probably, bumblebees are unable to distinguish flowers of different color at distances greater than 0.2–0.7 m (Wagner 1907; Kugler 1943). In addition, the low spatial resolution of the insect eye (Autrum 1952; von Frisch 1965; Dafni et al. 1997) limits the discrimination of small objects, like flowers. Hence, from long distances (greater than approximately 0.3 m), the whole plant seems to represent one single unit (Knoll 1926; Fægri and van der Pijl 1976; Dafni et al. 1997). Only after reaching the plant can insects distinguish between individual flowers and their colors and make a color choice. Since we found no effect of plant density on the approach rate, we conclude that the plants observed in our study appeared as single long-distance attraction units to the insects.

A number of hypotheses exist for the functional significance of floral color change (Weiss and Lamont 1997). In P. collina, we assume that the benefit is mainly an increased overall attractiveness combined with the ability to lead pollinators to reproductive flowers. This benefit is based on the occurrence of floral color change, amount of reward, and residual reproductive ability. This correlation may contribute to increasing male and female plant fitness by reducing the conflict between long- and short-distance attraction of pollinators.

To illustrate this benefit of floral color change for plants pollinated by visually oriented animals, we compare four potential scenarios in which the size and color of the plant floral displays vary. First, plants do not maintain their flowers beyond their reproductive period and the petals wither or drop. Compared to the following scenarios, these plants have the disadvantage of lower long-distance attractiveness. However, there is no risk of visits to non-reproductive flowers (see below).

Second, the plants do maintain flowers beyond their reproductive period, but these flowers remain unchanged in nectar production and color. In this case, the plants would benefit from increased long-distance attraction due to a large floral display. However, because young reproductive and old post-reproductive flowers appear the same to flower visitors, the plants would suffer an increased risk of pollinators visiting post-reproductive flowers and, consequently, waste both imported outcross pollen (reduced female fitness) and already collected self-pollen (reduced male fitness).

Third, plants maintain non-reproductive flowers but with a lower nectar production and with the same color. In this case, the risk of decreased fitness as in the second scenario is reduced by a correlation between the residual reproductive ability and the amount of reward offered in the flowers. Lower rewards should reduce the short-dis-
Table 3 Overview of plant species studied for correlations between floral color change and other floral events: Color choice flower visitors preferred young, unchanged flowers; Reward decline old, changed flowers contained less reward than young ones; Decreased reproductive ability old, changed flowers had a lower residual female reproductive ability due to pollination or lost fertility

<table>
<thead>
<tr>
<th>Species</th>
<th>Color choice</th>
<th>Reward decline</th>
<th>Decreased reproductive ability</th>
<th>Reference</th>
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<td>Aesculus hippocastanum</td>
<td>Yes</td>
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<tr>
<td>Anchusa stringosa</td>
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<td>Arnebia echioides</td>
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<td>Banksia ilicifolia</td>
<td>Yes</td>
<td>Yes</td>
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<tr>
<td>Caesalpinia eriostachys</td>
<td>Yes</td>
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<td>Jones and Buchmann 1974</td>
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<td>Caesalpinia pulcherrima</td>
<td>Yes</td>
<td>Yes</td>
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<td>Cruden and Hermann-Parker 1979</td>
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<td>Yes</td>
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<td>Casper and LaPine 1984</td>
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<td>Erythroxylum megacarpum</td>
<td>Yes</td>
<td>Yes</td>
<td></td>
<td>Lamont 1985</td>
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<tr>
<td>Fuchsia excorticata</td>
<td>Yes</td>
<td>Yes</td>
<td></td>
<td>Delph and Lively 1989</td>
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<td>Grevillea pilulifera</td>
<td>Yes</td>
<td>Yes</td>
<td></td>
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<td>Hypocalymma angustifolium</td>
<td>Yes</td>
<td>Yes</td>
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<td>Isopegon dubius</td>
<td>Yes</td>
<td>Yes</td>
<td></td>
<td>Schemske 1980</td>
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<tr>
<td>Lantana camara</td>
<td>Yes</td>
<td>Yes</td>
<td></td>
<td>Barrows 1976, Weiss 1991</td>
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<td>Lantana trifolia</td>
<td>Yes</td>
<td>Yes</td>
<td></td>
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<td>Lupinus argenteus</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
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</tr>
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<td>Lupinus arizonicus</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>Wainwright 1978</td>
</tr>
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<td>Lupinus blumeri</td>
<td>Yes</td>
<td>Yes</td>
<td></td>
<td>see Gori 1983</td>
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<td>Lupinus nanus</td>
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<td>Yes</td>
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<td>see Gori 1983</td>
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<td>Lupinus pilosus</td>
<td>Yes</td>
<td>Yes</td>
<td></td>
<td>Ne’eman and Nesher 1995</td>
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<td>Lupinus sparsiflorus</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
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<td>Lupinus texenis</td>
<td>Yes</td>
<td>Yes</td>
<td></td>
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<td>Melampyrum ciliare</td>
<td>Yes</td>
<td>Yes</td>
<td></td>
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<td>Mertensia spp.</td>
<td>No</td>
<td>Yes</td>
<td></td>
<td>Kevan 1978, see Gori 1983</td>
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<td>Myosotis colensoi</td>
<td>Yes</td>
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<td>Yes</td>
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<td>Oenothera drummondii</td>
<td>Yes</td>
<td>Yes</td>
<td></td>
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<td>Oxypopis splendis</td>
<td>Yes</td>
<td>Yes</td>
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<td>Parkinsonia aculeata</td>
<td>Yes</td>
<td>Yes</td>
<td></td>
<td>Jones and Buchmann 1974</td>
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<tr>
<td>Petrophile biloba</td>
<td>Yes</td>
<td>Yes</td>
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<td>Phyla incisa</td>
<td>Yes</td>
<td>Yes</td>
<td></td>
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<td>Pulmonaria officinalis</td>
<td>Yes</td>
<td>Yes</td>
<td></td>
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<td>Quisqualis indica</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
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<td>Ribes aureum</td>
<td>Yes</td>
<td>Yes</td>
<td></td>
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<td>Senecio jacobaea</td>
<td>Yes</td>
<td>Yes</td>
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<td>Verticordia chrysanthae</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
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<td>Verticordia huegeli</td>
<td>Yes</td>
<td>Yes</td>
<td></td>
<td>Lamont 1985</td>
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Tolerance attraction, indicated by shorter visiting bouts on the plants (Schemske 1980; de Jong et al. 1993; Klinkhamer and de Jong 1993). Only a few successive visits might be adequate for a plant, since most of the imported outcross pollen is deposited during the first few visits of a visiting bout (Thomson and Plowright 1980; Hesing 1988; Robertson 1992; de Jong et al. 1993; Harder and Wilson 1994; Rademaker et al. 1997). However, in this scenario, the pollinators are not directed to the young reproductive flowers. Therefore, a certain risk exits that pollinators leave the plant before visiting enough young rewarding and reproductive flowers. This could result both in reduced female fitness due to outcross pollen being deposited on no or on only a few receptive stigmas and in reduced male fitness due to smaller own-pollen loads on the pollinators. For plants with a large fraction of post-changed flowers, this risk should be high.

Fourth, the case of lungwort, the plants signal their old changed flowers visually by a changed flower color. Thus, the combination of a lower amount of reward and floral color change enables plants to direct pollinators which are able to learn the color cue to their reproductive flowers. In this way, plants may increase the probability of receiving outcross pollen on unpollinated stigmas (Schaal and Leverich 1980; Weiss and Lamont 1997). Furthermore, export of self-pollen can be in-
increased by insects visiting flowers that contain many and young pollen grains (pollen grains lose their ability to germinate while aging; Smith-Huerta and Vasek 1984; Thomson and Thomson 1992). In addition, discouraging pollinators from visiting post-reproductive flowers can increase male fitness by avoiding geitonogamous pollen wastage (Klinkhamer and de Jong 1993).

In other words, lungwort plants might minimize the dilemma stated by Hessing (1988) and Klinkhamer and de Jong (1993): how to get many pollinator approaches but only a limited number of flower visits? For lungwort plants, all flowers contribute to their long-distance, but mainly red ones to their short-distance attractiveness. In the phase of approaching a plant, all flowers regardless of color seem to represent a unit for foraging insects. Red and blue flowers contributed equally well to attract insects to the plants, but at the plant, the animals were able to distinguish differently colored flowers and visited mainly the highly rewarding red flowers. Thus, the co-occurrence of color change, residual reproductive ability, amount of reward, and color choice behavior of pollinators might optimize the attraction of pollinators by attracting many pollinators to the plant and simultaneously limiting the visits to pre-changed flowers.

This co-occurrence appears to be a general phenomenon. In most of the plant species studied so far, even for bird-pollinated plants, this pattern of floral events was found (Heinrich 1975; Schemske 1980). An overview of the results of these studies is given in Table 3. Therefore, we assume that the proposed mechanism of floral color change and its co-occurrence with amount of reward and reproductive ability play an important role for a large number of plant species. This advantage of reducing the conflict between long- and short-distance attraction has possibly made floral color change a common phenomenon in the plant kingdom.

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