

Sex related colour polymorphism  
in *Antennaria dioica*

by

Tove von Euler

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Department of Botany  
Stockholm University

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Plant Ecology  
Department of Botany  
Stockholm University  
S-106 91 Stockholm  
Sweden

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Cover: Pink and white females of *Antennaria dioica* in a seminatural grassland in Södermanland. Photo by Mathias Öster

## Summary

Insect pollinated plants often use flower colour to attract pollinators. Colour polymorphism, where flower colour varies between individuals of the same population, occurs in many species throughout the angiosperms. One is *Antennaria dioica*, which is often described as having white male flowers and pink or red female flowers. However, field observations of the species indicate that all three colour morphs occur in both sexes. Having two or more colour morphs within one population could invoke strong selective pressure. Based on floral reward or other morphological differences, pollinators may prefer one colour morph to another, affecting its relative fitness within a population. The aim of this project was to study colour morph distribution and to examine possible factors maintaining colour polymorphism in *A. dioica*. There was a similar pattern of colour morph distribution in all studied areas, with the white morph generally dominating among male individuals and the pink morph dominating among female individuals. There was no notable difference regarding the frequency of pollinator visits to male and female flowers. Nor was there any significant difference in seed production or pollen limitation between the two morphs. However, pink females had more ovules per flower head than white females.

## Sammanfattning

Insektspollinerade växter använder sig ofta av färger för att attrahera pollinatörer. Färgpolymorfism, där blomfärg varierar mellan olika individer inom samma population, förekommer hos många arter av angiospermer. En av dem är *Antennaria dioica*, där hanblommorna ofta beskrivs som vita, medan honorna beskrivs som rosa eller röda. I själva verket förekommer alla tre färgvarianterna hos båda könen. Förekomsten av två eller fler färgvarianter inom samma population skulle kunna utöva starkt selektionstryck på den relativa fördelningen av färgmorfer. Skillnader i resurser eller andra morfologiska skillnader kan leda till att pollinatörerna föredrar en färgvariant framför andra, vilket skulle påverka de olika färgmorfernas relativa fitness. Syftet var att studera fördelningen av färgvarianter och undersöka tänkbara faktorer som bidrar till att upprätthålla färgpolymorfismen hos *A. dioica*. Det fanns ett generellt mönster i fördelningen av de olika färgvarianterna mellan olika populationer, där den vita färgen var vanligast bland hanar och den rosa vanligast bland honor. Det var ingen skillnad i pollinatörsbesök mellan han- och honblommor. Inte heller fanns någon skillnad i fröproduktion eller pollenbegränsning mellan rosa och vita honor. Däremot hade rosa honor generellt fler ovuler per blomkorg än vita honor.

## **Introduction**

In plants, colours often provide important tools for attracting pollinators. Although there are many ways of communication between plants and their pollinators, such as size, shape, patterns, odour etc., colour is thought to be the strongest visual stimulus attracting insect pollinators (Gumbert 2000). It is generally agreed that, in order to optimise their fitness, insect pollinated flowers use visual cues to make sure that visiting pollinators recognise and visit other members of that particular species and discriminate against other species (Hemborg & Bond 2005). In some cases, however, there are large variations in flower colour within the same species. This phenomenon is referred to as colour polymorphism, and occurs in many species throughout the angiosperms. Colour polymorphism has been studied by evolutionary biologists since the 1970's, and is defined as the presence of two or more distinct, genetically determined colour morphs within a single interbreeding population, the rarest of which is too frequent to be solely the result of recurrent mutation (Jersáková et al. 2006; Gray & McKinnon 2006).

### *Selective responses to colour polymorphism*

The occurrence of two or more different colour variants within one plant population could invoke strong selective pressure. Niovi Jones & Reithel (2001) suggest three ways in which pollinators may respond to variation in floral morphology within a plant population: One of the alternative morphs may receive (1) more plant visits, (2) more flower visits per plant visit, and/or (3) longer visits. Any of these pollinator responses may influence the relative fitness of the alternative floral morphs (Niovi Jones & Reithel, 2001). One factor that may influence the fitness of a specific colour is its relative frequency within a population, affecting the magnitude and even the direction of pollinator preferences. The process where selection of a specific genotype depends on whether it is common or rare in a population is called frequency-dependent selection, and has been used to explain colour polymorphism in a number of cases. For example, there is evidence that bumblebees prefer more common colour morphs, independent of floral density, when flowers are rewarding. When the common morph is emptied of nectar, however, bumblebees can learn to avoid it (Smithson & Macnair 1997). Another case where frequency-dependent selection is suggested to occur is in the rewardless orchid *Dactylorhiza sambucina*. This species displays red, yellow and pink flowers and attracts pollinators by deceptive mimicry. Here, colour polymorphism is assumed to be maintained by pollinators who, having visited a flower without reward, search for a reward in a flower of a different colour (Pellegrino et al. 2005a). Since pollinators more often lack

previous experience of the rare morph, it is prone to receive relatively more visits than the more common morph. Provided that pollinators tend to visit the colour morph that most closely resembles the most recent rewarding flower they visited (pollinator constancy), selection may not only depend on the colour-morph frequency within the population, but also on the frequency of other similar looking rewarding species in the area (Jersáková et al. 2006).

However, frequency-dependent selection on colour polymorphisms is likely to be extremely difficult to discern in natural populations because of other factors that influence morph reproductive success (Jersáková et al. 2006). For instance, physiological properties affecting reproductive success may be linked to specific colour morphs. A difference in seed viability has been observed between two colour morphs of *D. sambucina*, where seeds produced by the purple morph were significantly heavier than those of the yellow morph (Jersáková et al. 2006). Moreover, there is evidence of so called post-pollination barriers, that inhibit reproductive success when crossing certain colour morphs, as a possible mechanism maintaining colour polymorphism in *D. sambucina* (Pellegrino et al. 2005b). Also, stochastic factors, such as demographic stochasticity, genetic drift and temporal environmental stochasticity, may randomly modify morph frequencies, population flowering patterns and plant-pollinator interactions, and therefore affect reproductive success, especially in extremely small populations. There may also be among-site variability of a broad range of abiotic (e.g. soil moisture, nutrients, climate) and biotic (e.g. vegetation, abundance of reward-producing flower species, pollinator abundance, predation) factors affecting selection on colour morphs (van Rossum et al. 2006).

#### *Morphological differences in dioecious species*

The evolution of floral trait variations is strictly linked to plant mating patterns (Pellegrino et al. 2005b). For small populations of dioecious species, efficient signalling is crucial in order to attract pollinators to members of both sexes within the species. Nevertheless, morphological variations between males and females are common among dioecious plants. One theory on this type of sex related polymorphism, proposed by Vamosi & Otto (2002), is that, in order to maximise their fitness, male flowers invest more in pollinator attractiveness whereas females invest more in ovule and seed production. They argue that the evolution of floral display is constrained by a resource allocation trade-off between display, which affects a plant's attractiveness to pollinators, and reproductive structures, such as pollen, ovules and

seeds. In dioecious plants, this trade-off may take on different forms in males and in females. For instance, if ample resources are devoted to reproductive structures in male individuals, and excess pollen is produced, a slight reduction in pollen production may have little effect on the amount of viable pollen that would attach to a pollinator. In female plants, however, even a slight reduction in ovule production may have significant negative effects on their fitness. These differences in resource allocation may in turn lead to differences in floral display and reward production between males and females (Vamosi & Otto 2002).

When the male and the female morph have different flower colour, pollinators may be able to distinguish male flowers from female ones. Since male flowers offer pollen, they tend to be more attractive to pollinators. This has been highlighted in a study on *Antennaria parvifolia*, where female inflorescences are actively discriminated against by flower visitors. Not only were female flowers less frequently visited; pollinators also tended to spend less time visiting each female flower (Bierzychudek 1987). In a study on *Silene dioica*, pollinators were reported to visit male flowers 3-4 times more often than female flowers (Carlsson-Granér et al. 1998). A contrasting theory on sex related polymorphism is that some species use colour polymorphism to advertise different rewards. To compensate for a lack of pollen, female flowers may offer other important resources to their pollinators. In *Leucadendron* (Proteaceae), male flowers offer food supplies and breeding sites to their pollinators, whereas female flowers offer shelter (Hemborg & Bond 2005). In this case, it is useful for the flowers to display different colours, advertising different essential rewards.

#### *Effects of isolation on dioecious species*

Dioecious species are particularly dependent on pollinators for their reproductive success (Carlsson-Granér et al. 1998). Fragmentation of the landscape increases the occurrence of small, isolated populations of dioecious species. If pollinator abundance subsequently declines, dioecious populations are at greater risk of extinction because pollinators may fail to visit less attractive female plants (Vamosi & Otto 2002). In many natural populations, seed set can be limited by the effectiveness of pollinators. Many studies have demonstrated that seed production increases as a result of hand pollination (Bierzychudek 1987) and studies on dioecious species have shown that seed set decreases with distance to the nearest male (Eriksson & Kiviniemi 1999; de Jong et al. 2005; Öster & Eriksson 2007). de Jong et al. (2005) offer two possible explanations for decreased seed set with distance. One is that

isolated plants receive fewer visits from pollinators and the other is that the quality of the visits decreases with distance to nearest male (de Jong et al. 2005).

#### *Flower colour polymorphism in Antennaria dioica*

*Antennaria dioica* is a dioecious perennial herb displaying colour polymorphism. It occurs in Europe and Asia in nutrient-poor areas and is a quite common herb in Swedish seminatural grasslands. In modern floras, *A. dioica* is often described as having white male flowers and pink or red female flowers (Krok & Almquist 2001; Mossberg & Stenberg 2003). However, field observations of the species indicate that this is not quite correct. In fact, although there is a greater tendency for male individuals to be white and females to be pink, all three colour morphs occur in both sexes (Bohlin 2006). This was observed as early as 1930 by the German botanist G. von Ubisch, who wrote: “When *A. dioica* appears in large numbers, one can often find representatives of all colours, ranging from white to red, within both sexes, although the male plants tend to be lighter on average than the female plants”. von Ubisch studied populations of *A. dioica* in 13 different areas in Germany, Norway and Slovakia. In twelve of those populations, he found that the dark red colour morph was more common in females than in males, and in eleven populations, the white colour morph was more common in males than in females (von Ubisch 1930).

In *A. dioica*, flowers of both sexes offer nectar as a reward to pollinators. Since the males also offer pollen, however, certain pollen-eating insects may specialise on male flowers and discard the female ones. If male flowers, among which the white colour morph is dominating, receive more pollinator visits than female flowers, the relative frequency of the colour morphs within a population may be affected by pollinator behaviour. The white colour may be more attractive to pollinators than the pink colour, provided that pollinators are able to distinguish between the different colours. At low pollinator abundance, sexual dimorphism often poses a problem to dioecious plants, in that it may easily result in pollination failure in female plants, which are often less attractive to pollinators. In the case of *A. dioica*, it may thus be profitable for females to be white, mimicking male appearance, to attract more pollinators. In that case, comparing females of the white and the pink colour morph, one would expect to find that white females have a higher rate of pollinator visits than pink ones.

The aim of this project is to examine the mechanisms maintaining colour polymorphism in *A. dioica*. The main questions asked are: 1) Are there differences in colour morph frequencies

among populations and, if this is the case, is there any evidence of frequency dependent selection? 2) Is there a difference in seed production between white and pink females? 3) Are male flowers more frequently visited by pollinators than females? 4) Are white females generally less pollen limited than pink females?

## Material and methods

### *Study species*

*Antennaria dioica* (L.) Gaertn. (Asteraceae: Gnaphalidae) is a dioecious, mat-forming, clonal, perennial herb found in Europe and Asia in nutrient-poor environments, such as heaths, dry grassland and sandy or stony places. It is favoured by cattle grazing, and is often found in seminatural grasslands (Tutin et al. 1976). In Sweden, *A. dioica* has declined during the 1900's due to a general decrease in seminatural grasslands. The flowers differ in colour from white to dark red. All flowers on one individual are of the same colour, which indicates that there is a genetic basis to the variation (Rydberg & Wanntorp 2001).

### *Study area*

The study was performed in seven seminatural grassland areas, maintained by cattle or sheep grazing, in the county of Södermanland in south-eastern Sweden (table 1). Södermanland is a varying landscape, made up of farmland, forest, rock, swamps and lakes. The flora of the seminatural grasslands in Södermanland is still quite diverse, at least in areas that have not been treated with nitrogen fertilizers (Rydberg 1991). All seven sites were situated within 10 km from each other.

**Table 1.** Location, areal, number of patches and number of flowering ramets of *Antennaria dioica* in seven semi-natural grasslands in Södermanland.

<i>site</i>	<i>area (ha)</i>	<i>n. of patches</i>	<i>n. of ramets</i>
Björktorp, Länna	6.8	7	5786
Lida, Vårfruberga	8.4	5	1373
St Askrännilen 2, Härad	3.7	5	2472
St Askrännilen 3, Härad	4.0	2	1423
St Trana 1, Åker	2.4	5	4855
Stämtorp, Länna	11.4	9	10453
säby 1, Aspö	11.0	5	4387

### *Colour morph frequencies and reproductive success*

In the seven examined grasslands, all flowering ramets of *A. dioica* were counted and categorised according to sex (male, female) and colour (red, pink, white). The number of genets of each type was also estimated (each small group of flowers of the same sex and colour was defined as one genet). To compare the reproductive success of females of the pink and the white colour morph, 9 patches were selected. A patch was defined as an isolated area rich in *A. dioica*, with a distance of at least 30 meters from a neighbouring patch. The selected patches were situated in Björkatorp (patch A,B,C,D), St Trana (patch E,F,G) and Stämtorp (patch H, I). The number of ramets occupying each patch ranged from 476 to 1822. For each patch, 40 pink and 40 white female ramets were marked. Because of their low abundance, individuals of the red colour morph were not included in the experiment.

To see if there were any differences in pollen limitation between the pink and the white colour morph, two patches (patch C, Björkatorp, and patch F, St Trana) with similar colour morph frequencies (~20% white females) were selected. A total of 320 flowering ramets were selected for the pollination experiment. For each ramet, height, number of flower heads and distance to nearest male were noted. In each patch, 80 female ramets of each colour morph were marked, where half of the plants were hand pollinated and the remaining plants were used as control. Pollen was added by brushing male flower heads (collected at least 25 m from the hand pollinated plant) against the recipient stigmas on the female flower heads. During one week, new flowering heads were pollinated as they started to bloom. During the counting of colour morphs and pollination experiment, the frequency of pollinator visits for each colour morph as well as the type of pollinator visiting the different morphs were recorded. Once the seeds were mature, at the end of June, the middle head of each marked ramet was collected. Fertilised and aborted seeds were then counted as a measure of reproductive success. For the pollination experiment, the seed set of the control group was compared with that of the group of plants exposed to hand pollination.

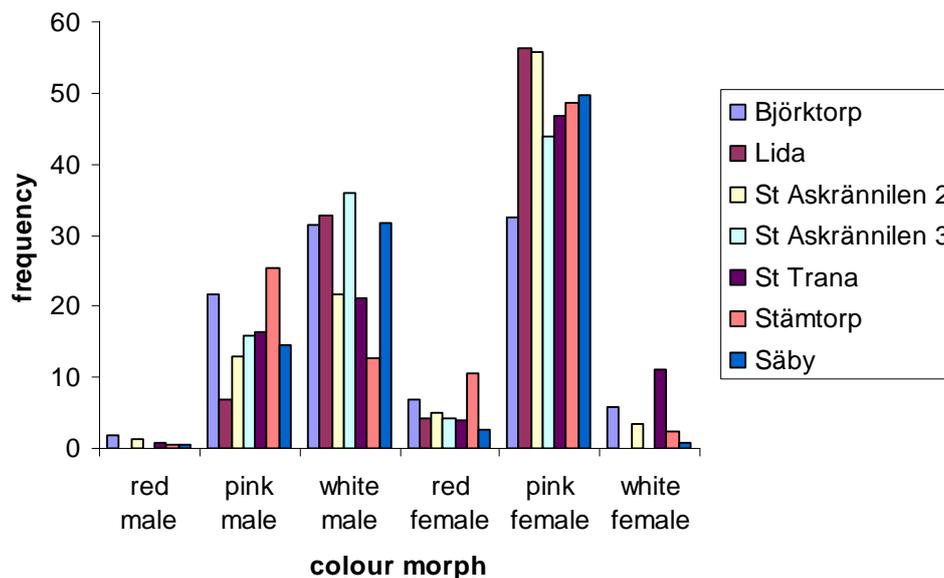
### *Statistical analysis*

The reproductive success of the two colour morphs, expressed as number of seeds or ovules per flower head in relation to colour, patch and pollination treatment was analysed using Anova. Fixed factors were colour, treatment and patch. Differences in pollinator abundance were tested using a chi-square test. The effect of distance to nearest male on pollen limitation was analysed using linear regression. All statistical analyses were performed in R 2.4.1.

## Results

### *Colour morph distribution*

There was a similar pattern of colour morph distribution in all studied areas, with the white morph generally dominating among male individuals and the pink morph dominating among female individuals. The patterns were the same on ramet- and genet level. All colour morphs were represented in all areas, except for two of the areas, where no red males or white females were found (fig. 1).

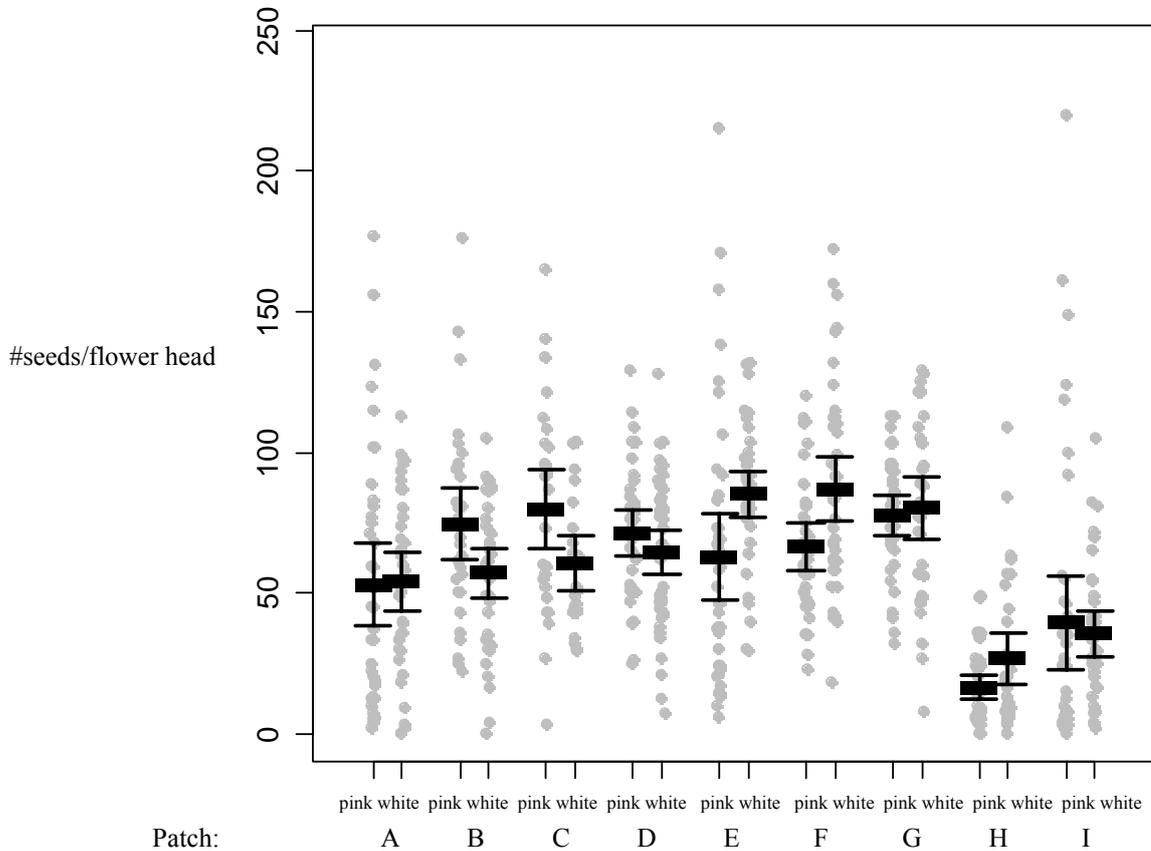


**Figure 1.** Relative frequency distribution of colour morphs of *Antennaria dioica* in the semi-natural grasslands Björktorp, Lida, St Askrännilen 2, St Askrännilen 3, St Trana, Stämtorp and Säby (Södermanland).

### *Reproductive success*

When all patches were considered, the relative fitness (number of seeds/flower head) of the colour morphs varied among different patches (fig. 2, table 2). In some patches, the white morph was more successful and in some patches, the pink morph was more successful. No general trend could be discerned as to which colour morph was most successful. Regarding the number of ovules produced, individuals of the pink morph produced more ovules per flower head than the white ones. Although the number of ovules also depended on an interaction between colour and patch (fig. 3, table 3), there was a highly significant difference

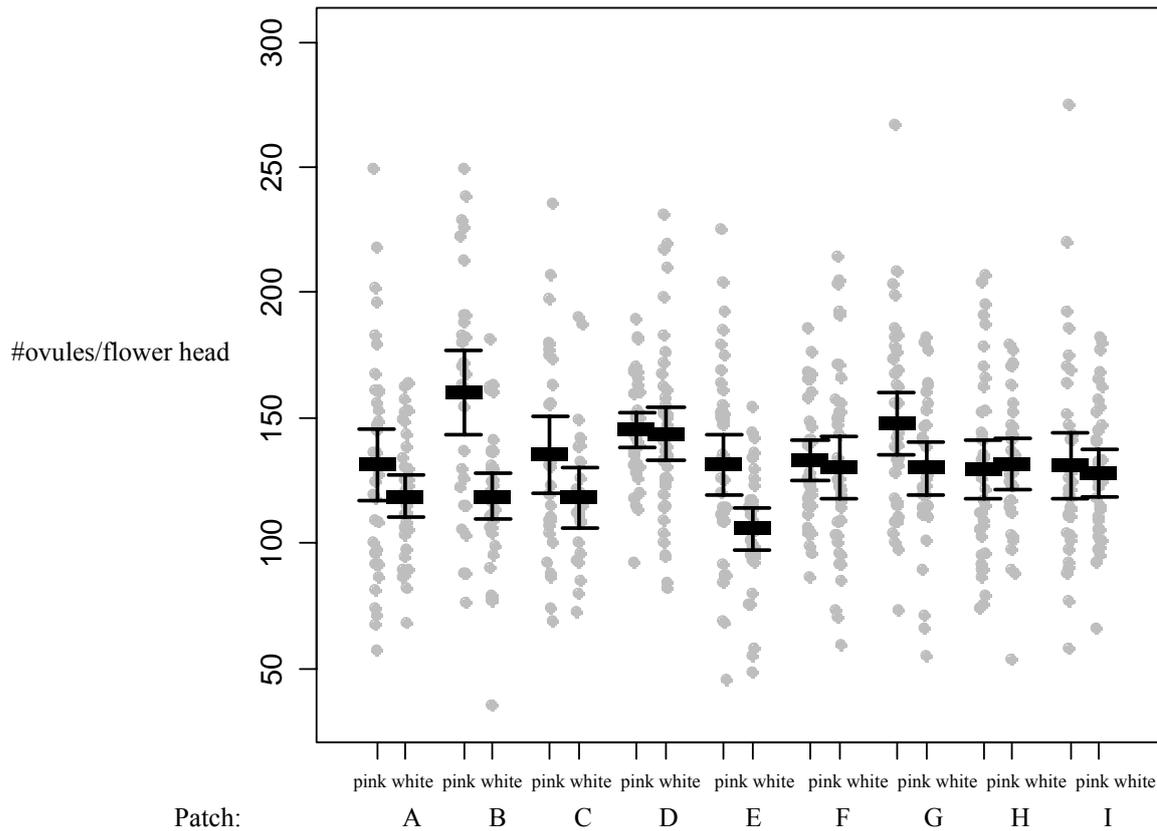
between the two colour morphs, where individuals of the pink morph produced around 10% more ovules than those of the white morph (table 3).



**Figure 2.** Number of mature seeds/flower head (■ mean,  $\top$  sd) in pink and white females of *Antennaria dioica* according to colour and patch.

**Table 2.** Number of seeds/flower head in pink and white females of *Antennaria dioica* in nine different patches in the semi-natural grasslands Björkatorp, St Trana and Stämtorp (Södermanland). Anova table (Type II tests).

	<i>Sum Sq</i>	<i>df</i>	<i>F</i>	<i>p</i>
colour	639	1	0.60	0.44
patch	229099	8	27.15	< 0.0001 ***
colour:patch	30898	8	3.66	< 0.0001 ***
Residuals	647			



**Figure 3.** Number of ovules/flower head (■ mean,  $\top$  sd) in pink and white females according to colour and patch.

**Table 3.** Number of ovules/flower head in pink and white *Antennaria dioica* in nine different patches in the semi-natural grasslands Björkatorp, St Trana and Stämtorp (Södermanland).

Anova Table (Type II tests)

	<i>Sum Sq</i>	<i>df</i>	<i>F</i>	<i>p</i>
colour	27555	1	23.59	< 0.0001***
patch	40455	8	4.33	< 0.0001***
colour:patch	28655	8	3.07	0.002**
Residuals	755754	647		

#### *Pollinator visits*

There was no notable difference regarding the frequency of visits to male and female flowers. The frequency of pollinator visits followed the same general pattern as the colour morph distribution of *A. dioica*, with an exception for the white female morph, where pollinator visitation was higher in relation to its frequency, and the pink female morph, where pollinator

abundance was slightly lower in relation to its frequency (table 4). The most common pollinators were Diptera. Other orders observed were Hymenoptera, Coleoptera and Lepidoptera. By far the most common pollinator was *Nematocera* (Diptera).

**Table 4.** Differences in the frequency of pollinator visits on *Antennaria dioica* in relation to colour morph frequency. The red colour morph was not represented due to its low abundance. Chi-squared test for given probabilities with simulated p-value (based on 10 000 replicates).  $p=0.0001$ . Significant differences between morphs are marked with \*.

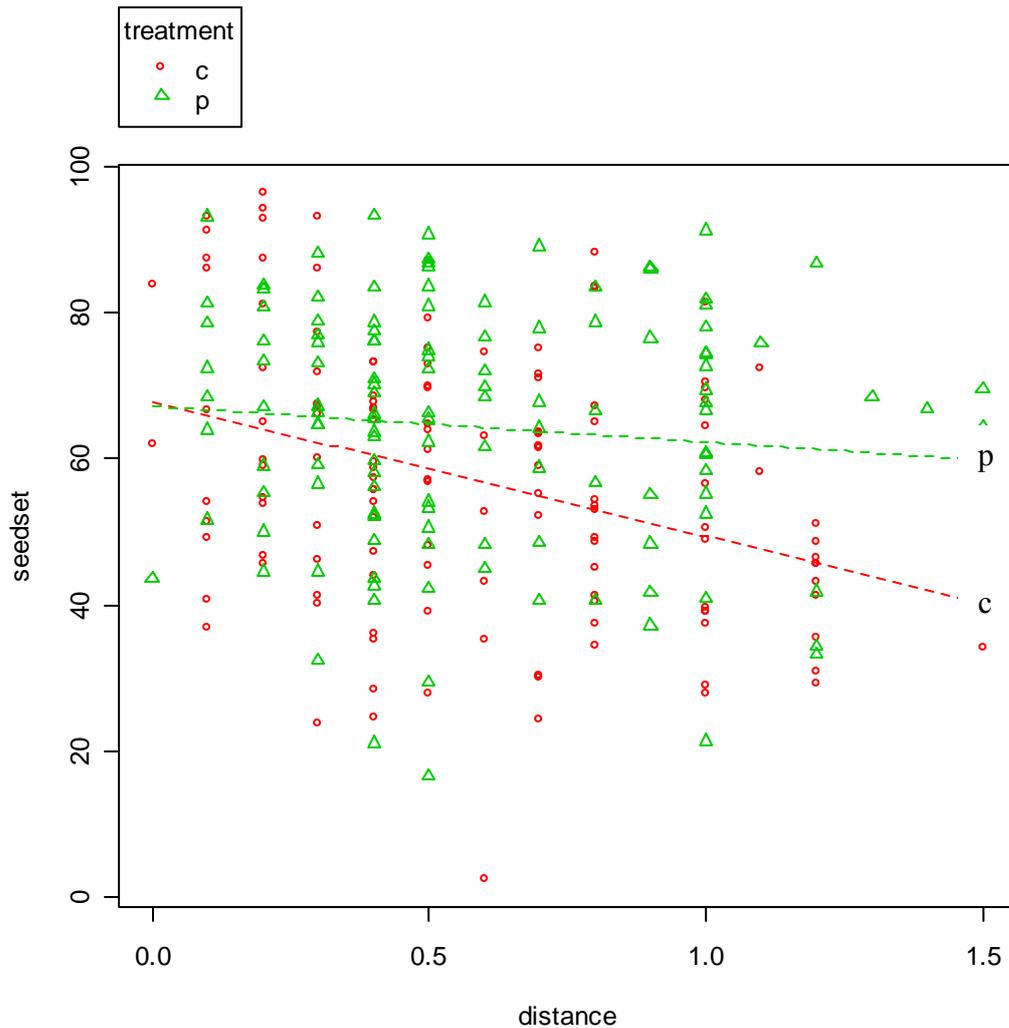
<i>sex</i>	<i>colour</i>	<i>morph frequency</i>	<i>pollinator frequency</i>
female	pink*	0.46	0.30
	white*	0.04	0.15
male	pink	0.19	0.24
	white	0.23	0.24

#### *Pollen limitation*

The results of the hand-pollination experiment showed that both colour morphs were pollen limited (table 5), but there was no significant difference regarding the extent of pollen limitation between the two morphs. Pollen limitation increased with distance to the nearest male ramet. For the control plants, seed-set was lower the longer the distance to the nearest male ( $t = -3.59$ ,  $df = 262$ ,  $p < 0.0001$  \*\*\*), whereas there was no such tendency among the hand-pollinated individuals (fig. 4). Even in the groups of hand-pollinated plants, seed-set did not reach 100% (table 5). The average number of flower heads was  $4.88 \pm 0.97$  for pink females and  $4.46 \pm 0.96$  for white females ( $t = 63.8$ ,  $df = 316$ ,  $p < 0.0001$  \*\*\*).

**Table 5.** Seed set for hand-pollinated and control plants in pink and white females of *Antennaria dioica* in two different patches in the semi-natural grasslands St Trana and Björktorp (Södermanland). Pink:  $t = 3.09$ ,  $p = 0.005$  \*\*. White:  $t = 2.88$ ,  $p = 0.026$  \*

	<i>pink females</i>		<i>white females</i>	
	control	pollinated	control	pollinated
st Trana	50%	58%	65%	70%
Björktorp	59%	67%	51%	61%



**Figure 4.** Seed set (%) as a function of distance (m) to nearest male in hand pollinated and control plants of *Antennaria dioica*.

## Discussion

### *Colour morph distribution*

With one exception, the distribution of the three colour morphs (white, pink, red) followed the same pattern in all studied areas, with the white morph most frequently occurring among males and the pink morph most frequently occurring among females. The fact that the rare colour morphs, such as white or dark red females and dark red males, were found in most of the studied areas suggests that they are indeed part of a pattern of colour polymorphism within both sexes, rather than being the result of rare mutations. Since colour morph distribution was the same in all but one studied area, frequency dependent selection could not be studied. To

be able to look for any frequency dependent selection between the two colours, it would probably be necessary to manipulate populations of *A. dioica*, creating a gradient of frequency distributions to compare pollinator preferences. Also, this experiment was performed within a quite small area. One may wish to perform larger regional studies to look for large-scale geographical variations to the colour morph distribution.

#### *Pollinator visits and pollen limitation*

The frequency of pollinator visits was noted parallel with the distribution, pollen limitation and reproductive success experiments. Contrary to previous findings on dioecious species, the total amount of pollinator visits was evenly distributed between the sexes; 160 on females and 167 on males. This contradicts the idea of male individuals of *A. dioica* being more attractive to pollinators. If male and female flowers are equally attractive to pollinators, there is no reason to believe that white females are white as a means of mimicking male flowers, and one would not expect to find white females being more frequently visited by pollinators than pink females. This is supported by the fact that there was no difference between the two colour morphs, neither in seed production nor in pollen limitation.

Regarding pollen limitation, the correlation between seed set and distance to nearest male shows that hand-pollination did increase seed set up to the same levels as in the most successful plants of the control group. Although both pink and white females were pollen limited, there was no difference in pollen limitation between the two colour morphs. This indicates that, in *A. dioica*, colour polymorphism may not be primarily pollinator-mediated. However, when comparing pollinator abundance with colour morph frequencies, white females received more pollinator visits in relation to their frequency whereas the pink females were less visited in relation to their frequency. The ambiguity of these results makes it difficult to draw conclusions concerning the role of pollinator behaviour in maintaining colour polymorphism in *A. dioica*.

There was, however, considerable variation in relative fitness, measured as seed production, between the pink and the white colour morph depending on location, which indicates that environmental factors, rather than pollinator preferences, may play an important role regarding the reproductive success of the colour morphs. Interestingly, although there was no significant difference in seed production between the colour morphs, female individuals of the pink colour morph produced significantly more ovules per flower head (ca 10% more than the

white ones). The fact that the pink females also had more flower heads per ramet further enhances this difference. It might be that the white morph is generally better suited to persist in varying environmental conditions (generalist) whereas the pink morph possesses greater resources and may flourish at optimal conditions (specialist). To sum up, the results of this study showed that the distribution of different colour morphs of *A. dioica* was similar in different areas. Contrary to the hypothesis, there was no difference in seed production between pink and white females and pollinators showed no preference for male flowers. Although both pink and white females turned out to be pollen limited, there was no difference in pollen limitation between the two colour morphs. There were, however, differences in number of ovules and number of flower heads between pink and white females. Instead of focusing on pollinator behaviour, it may be interesting to investigate if there are other factors influencing and maintaining colour polymorphism in *A. dioica*, such as differences in resources and tolerance towards environmental fluctuations.

## References

- Bierzychudek, P. (1987) Pollinators increase the cost of sex by avoiding female flowers. – *Ecology* 68:444-447.
- Bohlin, K. (2006) Olika färgmorfer hos Kattfot. – *Svensk Botanisk Tidskrift* 100:3.
- Carlsson-Granér, U., Elmqvist, T., Ågren, J., Gardfjell, H., Ingvarsson, P. (1998) Floral sex ratios, disease and seed set in dioecious *Silene dioica*. – *Journal of Ecology* 86:79-91.
- Eriksson, O. and Kiviniemi, K. (1999) Site occupancy, recruitment and extinction thresholds in grassland plants: an experimental study. – *Biological Conservation* 87:319-325.
- Gray, S.M. and McKinnon, J.S. (2006) Linking color polymorphism maintenance and speciation. – *Trends in Ecology and Evolution* 22:71-79.
- Gumbert, A. (2000) Color choices by bumble bees (*Bombus terrestris*): innate preferences and generalization after learning. – *Behavioral Ecology and Sociobiology* 48:36-43.
- Hemborg, Å.M. and Bond, W.J. (2005) Different rewards in female and male flowers can explain the evolution of sexual dimorphism in plants. – *Biological Journal of the Linnean Society* 85:97-109.
- Jersáková, J., Kindlmann, P., Renner, S.S. (2006) Is the colour dimorphism in *Dactylorhiza sambucina* maintained by differential seed viability instead of frequency-dependent selection? – *Folia Geobotanica* 41:61-76.

- de Jong, T.J., Batenburg, J.C., Klinkhamer, P.G.L. (2005) Distance-dependent pollen limitation of seed set in some insect-pollinated dioecious plants. – *Acta Oecologica* 28:331-335.
- Krok, Th.O.B.N. and Almquist, S. (2001) Svensk flora – Fanerogamer och ormbunsväxter. 28<sup>th</sup> edition. Liber förlag, Falköping.
- Mossberg, B. and Stenberg, L. (2003) Den nya nordiska floran. Wahlström & Widstrand, Stockholm.
- Niovi Jones, K. and Reithel, J.S. (2001) Pollinator-mediated selection on a flower color polymorphism in experimental populations of *Antirrhinum* (Scrophulariaceae). – *American Journal of Botany* 88:447-454.
- Pellegrino, G., Caimi, D., Noce, M.E., Musacchio, A. (2005a) Effects of local density and flower colour polymorphism on pollination and reproduction in the rewardless orchid *Dactylorhiza sambucina* (L.) Soó. - *Plant Systematics and Evolution* 251:119-129.
- Pellegrino, G., Bellusci, F., Musacchio, A. (2005b) Evidence of post-pollination barriers among three colour morphs of the deceptive orchid *Dactylorhiza sambucina* (L.) Soó. – *Sexual Plant Reproduction* 18:179-185.
- van Rossum, F., Campos de Sousa, S., Triest, L. (2006) Morph-specific differences in reproductive success in the distylous *Primula veris* in a context of habitat fragmentation. – *Acta Oecologica* 30:426-433.
- Rydberg, H. (1991) Naturen i Södermanland. Gummessons tryckeri AB, Falköping.
- Rydberg, H. and Wanntorp, H. (2001) Sörmlands flora. Botaniska sällskapet i Stockholm.
- Smithson, A. and Macnair, M.R. (1997) Density-dependent and frequency-dependent selection by bumblebees *Bombus terrestris* (L.) (Hymenoptera: Apidae). – *Biological Journal of the Linnean Society* 60:401-417.
- Tutin, T.G., Heywood, V.H., Burges, N.A., Moore, D.M., Valentine, D.H., Walters, S.M. & Webb, D.A. (1976) *Flora Europaea, Vol. 4. Plantaginaceae to Compositae (and Rubiaceae)*. Cambridge University Press, Cambridge.
- von Ubisch, G. (1930) Geschlechtsverteilung und sekundäre Geschlechtsmerkmale bei *Antennaria dioica* (Gaertn.). – *Biologisches Zentralblatt* 50:532-540.
- Vamosi, J.C. and Otto, S.P. (2002) When looks can kill: the evolution of sexually dimorphic floral display and the extinction of dioecious plants. - *Proceedings of the Royal Society of London Series B* 269:1187-1194.
- Öster, M. and Eriksson, O. (2007) Sex ratio mediated pollen limitation in the dioecious herb *Antennaria dioica*. – *Ecoscience* (in press).

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