

## Variation in floral morphology and individual fecundity in *Erythronium dens-canis* (Liliaceae)

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This study investigated the extent to which the reproductive success of plants of *Erythronium dens-canis* (Liliaceae), a spring herb of mountain habitats, is dependent on floral morphology. To this end, a series of studies was performed in an area in northwest Spain. The results show that *E. dens-canis* plants in this area a) are self-compatible, b) need pollinator visits (largely *Bombus terrestris* and *Andrena* spp.) to produce seed, and c) show high fruit set under natural conditions. Only 20% of among-plant variance in floral morphology variables was explained by variation in plant size. Floral morphology variables (outer tepal length, stamen length, style length and ovule number) tend to vary in parallel, indicating the existence of an “integrated floral phenotype”. Two floral morphology variables (initial number of ovules and outer tepal length) had statistically significant or near-significant effects on seed production. A more detailed experimental analysis indicated that small-flowered plants produce fewer seeds than large-flowered plants, and that this is attributable to less efficient pollination of small flowers. The results of this study thus suggest that among-plant variation in floral morphology in *E. dens-canis* has implications for reproductive success.

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Entomophilous plants regulate opportunities for mating via the effects of the morphology of flowers and inflorescences on pollinator attraction and behaviour, pollen dispersal and the incidence of selfing (Harder et al. 1985, Harder and Barrett 1996). If one or several pollinator species prefer a floral trait displayed by a subset of individuals in the population, or if a certain floral trait increases the precision of pollination, then that trait may influence reproductive success (“phenotypic selection”). If furthermore that trait is genetically controlled, there may be selection for particular floral types (“evolutionary response to selection”) (see e.g. Herrera 1993).

The influence of floral traits on fruit and/or seed production has been documented in numerous entomophilous species (Herrera 1990, 1993, Wilson and

Thomson 1996, references cited in these studies). Such influences may reflect differences in pollinator attraction (e.g. larger flowers are more attractive) or in physiological reproductive potential (e.g. larger flowers have more ovules). In addition, floral traits may influence male reproductive success (i.e. efficiency of pollen export) (Young and Stanton 1990). Both female and male reproductive success may be influenced by physiological costs (structural carbohydrates required for petals, sugars for nectar, nitrogen and phosphorus in pollen, etc.), by differential access to resources (spatiotemporal advantages related to flower position or day of anthesis, independently of floral morphology), and/or by differences in the effectiveness of pollination among flowers at different positions (Lee 1988, Galen et al. 1993, Ashman 1994, Diggle 1995, Galen 1996).

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In situations in which seed production is limited by pollinator availability, the consequences of differences in pollinator attraction may be particularly marked. Reduced fecundity as a result of pollination limitations has been observed in species with different reproductive mechanisms and from various habitats (Burd 1994). Such reductions may be due to pollinator scarcity or to limitations on the amount of pollen transferred. Plants in habitats with harsh climate and/or that reproduce in winter are particularly likely to be the subject to pollination limitations. This has been documented in early-flowering species (Motten 1986). More generally, pollination frequency in a number of species has been shown to vary among years, among seasons or within the reproductive period (Galen 1985, Johnston 1991, Widén 1991, Murphy and Vasseur 1994, Ramsey 1995). The effects of pollination on fecundity may also be dependent on the plant's sexual system, since self-compatible plants can respond to pollen scarcity by selfing, and in this way at least partially restore fecundity.

In this study we investigated the relationship between flower morphology and female reproductive success in a population of *Erythronium dens-canis* (Liliaceae) at the western extreme of the Cantabrian Cordillera in northern Spain. We addressed three specific questions. First, how much does floral morphology vary, and how are different morphometric variables related to one another? Second, is floral morphology related to fecundity under natural pollination conditions? Third, to what extent are individual differences in reproductive success related to differences in the amount of pollen received? Throughout the three-year study period (1996–1998), we also investigated other aspects of this species' reproductive biology.

We selected *E. dens-canis* as study species for two main reasons. First, it has a single flower; the additional effects of between-flower and between-fruit competition are thus avoided. Second, it is a winter-flowering species that occurs in mountain habitats, and might therefore be expected to suffer from a low frequency of pollinator visits.

## Methods

### The study area and species

The study was performed in the Sierra del Caurel (Lugo) at the western extreme of the Cantabrian Cordillera, in northwest Spain, during winter and spring of the years 1996–1998. The populations studied are located at altitudes of between 1400 and 1500 m a.s.l., near to the "Bosque de la Rogueira", in an area with mixed woodland, dominated by *Sorbus aucuparia* L. and *Betula celtiberica* Rothm. & Vasc. and showing varying degrees of disturbance. The *E. dens-canis* plants grow in clearings in scrub dominated by *Erica australis* L. and *Erica arborea* L.

*Erythronium dens-canis* L. (Liliaceae) is a bulbous geophyte developing in winter and spring. Plants produce a single pink flower. It is endemic to Europe. Reproductively mature individuals are 10–30 cm high, with two opposite leaves at the base of the scape, and three stigmas that exert to varying distances (so that flowers are herkogamous). The stamens are arranged at two levels. Those of the first level (i.e. the three shortest stamens) open on the first day of anthesis. Subsequently, the second-level stamens open and the tepals retract, leaving the style exerted. The duration of these phases varies depending on climatic conditions and whether or not the flower has been pollinated. Stamen length was positively correlated with the number of pollen grains ( $r = 0.8$ ,  $p < 0.01$ ). Stigmas became receptive on the day the flower opened (i.e. the day the first level of stamens opened); the plants are therefore adichogamous (Gutián unpubl.).

Flowering begins in March. The fruit is a capsule containing numerous elaiosome-bearing ant-dispersed seeds. The capsules dehisce in June. In both cases significant among-year variation was observed (Fig. 1). Fruit set in our study populations is consistently 100%, and seed set ca 44%, with very little variation among populations. Severe loss of young capsules occur as a result of herbivory by ungulates (Gutián unpubl.).

The biology of this species is poorly understood, unlike that of non-European species of the genus, about which considerable information exists (Motten 1983, 1986, Wolfe 1983, Thomson and Stratton 1985, Thomson 1986, Thomson and Thomson 1989, Cruzan 1990, Harder et al. 1993, Weiblen and Thomson 1995, Allen et al. 1996, Wilson and Thomson 1996, Cruzan and Thomson 1997).

### Breeding system and pollinator survey

In 1996, six plants were covered with muslin box-frames (50 × 50 × 50 cm) before the onset of flowering to investigate the degree of dependence of seed production on pollinators; our previous experience indicates

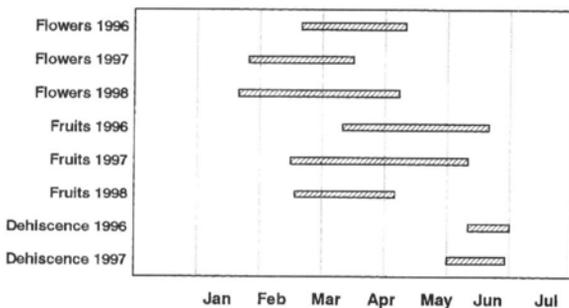


Fig. 1. Flowering and fruiting phenology of the study population of *E. dens-canis* over the three years of the study.

that box-frames of this type do not significantly affect the environmental conditions experienced by the plant. Another six plants were likewise covered with muslin box-frames, and manually pollinated on three consecutive days with self pollen, to investigate self-compatibility. In both cases, another six plants were assigned as controls. In 1997, to characterize the pollinator fauna, we performed twelve 30-min censuses at different times of day, in all cases sunny days, recording all visits and collecting all visitors for subsequent identification.

### Plant morphology

To characterize relationships between plant morphology variables, we used data from two groups of plants. In the first group ( $n = 20$ ), we measured leaf length, leaf width, leaf area (with an image analyser), and total weight of the plant after oven-drying at 50°C to constant weight; these data allowed investigation of possible relationships between biomass and leaf dimensions. In the second group ( $n = 50$ ), we measured the length and width of the largest leaf, together with outer tepal length, stamen length and style/stigma length; number of ovules per ovary was also determined with the aid of a stereo microscope. These data allowed investigation of the extent to which variations in floral morphology are attributable to variations in plant size.

### Floral morphology and reproductive success

To investigate possible relationships between floral morphology and female fecundity, we marked 80 randomly selected mature plants with metal tags. In the winter of 1996, for all plants we then measured size of the largest leaf, outer tepal length and stigma exertion distance (the distance that the stigma extends beyond the distal extreme of the anthers); in the rare cases in which the anthers extended beyond the stigmas, stigma exertion distance was recorded as a negative value. Plants were monitored until fruiting; before dehiscence, mature capsules were collected in separate vials and transferred to the laboratory. There they were opened, the seeds counted, and the number of aborted ovules determined with the aid of a stereo microscope. We also performed an experiment to investigate possible differences in reproductive success due to insufficient pollination of smaller flowers. Specifically, we marked 40 "large-flowered" plants (tepal length > 30 mm) and 40 "small-flowered" plants (tepal length < 25 mm); within each group 20 randomly selected plants were subjected to manual pollination with non-self pollen, while the remaining 20 plants served as unmanipulated controls. On each plant we measured tepal length with a digital calliper, and after flowering capsules were collected for determination of number of seeds and number of aborted ovules.

### Data analysis

Between-group comparisons were done by *t* tests or Mann-Whitney *U* tests (for comparisons of bagged plants with the corresponding controls). Possible relationships between variables were investigated by Pearson product-moment correlation analyses following confirmation of normality. To investigate the proportion of variance in flower morphology variables explained by plant size (as indicated by leaf length and width), we used canonical correlation analyses. To investigate whether flower morphometric variables covary, a principal components analysis was performed. The possible influence of morphometric variables (outer tepal length and stigma exertion distance) and number of ovules on fecundity was investigated by multiple regression analysis with number of seeds as dependent variable, following confirmation of data normality. The possibility that pollen limitations are more common among small-flowered plants than large-flowered plants was investigated with a two-way analysis of variance, with the fixed-effect factors flower size (large or small) and pollination treatment (manual cross-pollination vs control), their interaction, and the covariate initial number of ovules. All analyses were performed with the aid of SPSS (Anon. 1997).

## Results

### Breeding system and pollination survey

Flowers were visited mainly by *Bombus terrestris* (Apidae) (53% of the 38 visits observed) and an *Andrena* species (Andrenidae) (44% of visits); the remaining visit was by a lepidopteran (*Gonopteris rhamni* L.). Plants that were bagged to prevent pollinator access did set fruit but did not produce well-developed seeds. Plants were self-compatible: all flowers that were manually pollinated with self pollen produced fruit, and on average 39% of ovules in such flowers produced seed; this value does not differ significantly from that obtained for untreated control plants ( $U = 8.0$ ,  $p = 0.35$ ).

### Plant morphology

Table 1 shows descriptive statistics for the morphometric variables considered. The most variable character is number of ovules, and the least variable is style length (CV 28 and 9.8% respectively).

The proportion of the variation in flower morphology variables attributable to plant size was evaluated by canonical correlation analysis, considering the morphometric variables outer tepal length, stamen length, style length and number of ovules (variable set 1) and leaf length and leaf width (variable set 2) as indicators of

Table 1. Descriptive statistics for the morphometric variables considered in *Erythronium dens-canis*. Values for 80 plants. CV = coefficient of variation. OTL = outer tepal length.

	OTL	Style length	Stamen length	Leaf length	Leaf width	Ovule number
mean $\pm$ SD (mm)	25.6 $\pm$ 3.5	14.4 $\pm$ 1.4	17.7 $\pm$ 1.8	77.0 $\pm$ 17.2	17.2 $\pm$ 4.6	46.4 $\pm$ 13.0
Range (mm)	19.5–34.0	11–17	13.5–22.5	45.0–115.0	1.0–34.0	29–84
CV (%)	13.7	9.8	10.0	22.4	26.6	27.9

plant biomass ( $r = 0.81$ ,  $p < 0.0001$ , between leaf length and biomass;  $r = 0.85$ ,  $p < 0.0001$ , between leaf width and biomass). The coefficient of correlation between the two sets of variables was 0.66. Redundancy analysis indicated that leaf size (variable set 2) explained 20% of the variance in flower morphology variables, i.e. that 80% of the variance was independent of plant size.

The flower morphology data were then subjected to a principal components analysis with the aim of identifying the trends underlying the observed among-individual variation (see Herrera 1988 for a similar analysis). The first axis extracted explained 62% of total variance (Table 2). All flower morphology variables had high loadings on the first factor, indicating that the variables considered (outer tepal length, style length, stamen length and ovule number) tend to covary.

### Floral morphology and reproductive success

Of the 80 plants used to investigate relationships between floral morphology and reproductive success, 14 suffered significant herbivory during the study period; all remaining plants set fruit. Multiple regression analysis was used to investigate whether there was any relationship between the number of seeds per capsule and outer tepal length (OTL) and stigma exertion distance (SED). Squared terms (OTL  $\times$  OTL, SED  $\times$  SED) were included in the analysis to detect possible nonlinear relationships. Number of ovules was not included as a candidate predictor variable, to prevent possible problems due to correlation with number of seeds per capsule ( $r = 4.3$ ,  $p = 0.001$ ). The results of this analysis indicate that both OTL and OTL<sup>2</sup> had significant effects on number of seeds, suggesting a nonlinear relationship with OTL (Table 3). To rule out the possibility that the significant effect of OTL reflects an

indirect effect of number of ovules, we performed a general linear model (GLM) analysis with number of seeds as dependent variable and OTL, OTL<sup>2</sup> as well as the number of ovules as independent variables. The results indicate that number of ovules and OTL<sup>2</sup> had a significant effect, and OTL a marginally significant effect (Table 4).

Using analysis of variance to investigate the effects of flower size and pollination treatment on number of seeds, with number of ovules as covariate, indicated that number of ovules had a significant effect (Table 5). In our supplementary pollination experiments, the proportion of ovules producing seed after supplementary pollination was 46% in "large-flowered" plants and 47% in "small-flowered" plants, 44 and 39% respectively in control plants. Flower size by itself had a marginally significant effect; however, pollination treatment and the interaction between pollination treatment and flower size had significant effects, indicating that large and small flowers respond in different ways to supplementary pollination. Specifically, only small flowers showed a significant improvement in reproductive success following supplementary pollination; in other words, reproductive success is pollination-limited in small flowers but not in large flowers.

### Discussion

Like other members of the genus *Erythronium*, *E. dens-canis* is a spring herb; however, its reproductive biology differs from that of other species of the genus in various respects (Table 6). Seed production by *E. dens-canis* following selfing is similar to that observed following pollination under natural conditions. By contrast, seed production by *E. americanum* Ker Gawl. following selfing is significantly lower than following natural pollination (see Harder et al. 1985), while *E. umbilicatum* Parks & Hardin is self-incompatible (Motten 1983). All species are basically pollinated by hymenopterans, *E. americanum* and *E. umbilicatum* largely by *Apis* and *Andrena* species, *E. grandiflorum* Pursh by *Bombus* (basically by *B. occidentalis*), and *E. dens-canis* largely by *Bombus* and *Andrena* species. Seed set varies little between *E. americanum*, *E. umbilicatum* and *E. grandiflorum*, although number of ovules is markedly lower in *E. umbilicatum* (see Motten 1983, Harder et al. 1985).

Table 2. Summarized results of a principal components analysis of the floral variables matrix in *Erythronium dens-canis*, showing loadings of each variable on the first three axes extracted. OTL = outer tepal length.

Variable	Axis		
	I	II	III
OTL	0.777	-0.454	0.392
Style length	0.709	0.597	0.337
Stamen length	0.825	0.336	-0.396
Ovule number	0.829	-0.420	-0.262
% variance explained	61.85	21.31	12.32

Table 3. Results of multiple regression with number of seeds in the capsule as dependent variable and stigma exertion distance (SED) and outer tepal length (OTL) as independent variables. Squared terms (SED<sup>2</sup> and OTL<sup>2</sup>) were included as dependent variables to allow detection of nonlinear effects. b = partial regression coefficients;  $\beta$  = standardized partial regression coefficients.

	b	$\beta$	t	Significance level
Constant	108.917		2.172	0.034
SED	-0.485	-0.128	-0.385	0.702
SED <sup>2</sup>	0.121	0.266	0.798	0.428
OTL	-6.703	-3.129	-2.040	0.046
OTL <sup>2</sup>	0.117	3.391	2.217	0.030

Floral morphology variables (tepal size, stamen length, style length and number of ovules) tend to covary (i.e. the different variables are positively correlated), indicating the existence of an "integrated floral phenotype". In addition, larger flowers show more pronounced stigma exertion with respect to the distal extreme of the anthers. Herkogamy (i.e. spatial separation of stigmas and anthers) is widely considered to be a mechanism for reducing the probability of same-flower selfing in species in which stigma receptivity and pollen release occur simultaneously (Schoen 1982, Campbell et al. 1994). Thomson and Stratton (1985) have shown that a lower proportion of self pollen is typically present on the stigmas of *Erythronium* flowers with long styles than on the stigmas of flowers with short styles. Prior to the present study, the data available indicated that stigma exertion ranges from -0.1 mm in *E. americanum* (i.e. anthers extend beyond stigmas) to 1.5 mm in *E. grandiflorum*. The present results show that stigma exertion is ca 4.2 mm in our study population of *E. dens-canis*, and that this species is capable of producing seeds in the absence of pollinators. If we suppose that seeds produced by selfing are of lower quality than seed produced by cross-pollination, then it is reasonable to expect there to be selection for prefertilization isolation mechanisms – such as stigma exertion – to reduce the probability of selfing.

The results of our phenotypic analysis to investigate relationships between flower characteristics and reproductive success (number of seeds) show a significant effect of both outer tepal length (OTL) and OTL<sup>2</sup>. Similarly, GLM analysis indicated that the number of ovules and OTL<sup>2</sup> had significant effects, while OTL had a near-significant effect ( $p = 0.055$ ). This suggests that the observed differences in seed production per plant

Table 4. Results of generalized linear modelling (GLM) with number of seeds in the capsule as dependent variable and outer tepal length (OTL), OTL<sup>2</sup> and ovule number (ON) as independent variables.

Source	DF	F	Significance level
ON	1	8.821	0.004
OTL	1	3.809	0.055
OTL <sup>2</sup>	1	4334	0.041
error	62		

are not related only on number of ovules, but also to flower size.

Furthermore, the significant interaction between flower size and pollination treatment in our supplementary pollination experiment indicates that reproductive success is significantly improved by manual crossing only in the case of small flowers, not large flowers. Two non-exclusive explanations may be relevant here. First, small flowers may attract pollinators less effectively. Second, the effectiveness per visit may be lower in small flowers. In studies of other plants, it has been observed that certain *Bombus* species prefer large flowers, but pollen deposition is not necessarily more effective in such flowers (Stanton 1986, Galen and Newport 1987). Furthermore, it should always be kept in mind that the effects of a given floral morphology trait on pollen transfer may vary depending on which of a plant's various pollinator species is considered (the "interaction term" in pollination, sensu Wilson and Thomson 1996).

Our supplementary pollination experiments likewise indicated that overall reproductive success is limited by pollination level, suggesting that variations in reproductive success may reflect between-plant differences in traits related to pollination. Wilson (1995), in a study of *Drosera tracyi* Macfarlane, observed a wide range of levels of pollination and corresponding levels of selection, which was more intense at intermediate pollination frequencies. Young and Stanton (1990), in a study of *Raphanus raphanistrum* L., found that corolla size was an effective predictor of pollen export when pollination frequency was low, but not when pollination frequency was high. In the present study, we did not

Table 5. Results of analysis of variance to investigate the effects of flower size (large or small; see text) and pollination treatment (supplementary pollination vs no treatment) on number of seeds in the capsule.

Source of variation	DF	F	Significance level
Ovule number (covariate)	1	15.836	0.000
Flower size (FS)	1	3.222	0.080
Pollination treatment (PT)	1	4.729	0.035
FS $\times$ PT	1	5.472	0.024
Error	43		

Table 6. Summarized reproductive characteristics of species of the genus *Erythronium*, based on the present results (*E. dens-canis*) and previous studies (see text).

Species	<i>E. dens-canis</i>	<i>E. americanum</i>	<i>E. grandiflorum</i>	<i>E. umbilicatum</i>
Breeding system	Self compatible	Self compatible		Self incompatible
Pollinators	<i>Bombus</i> , <i>Andrena</i>	<i>Andrena</i> , <i>Apis</i>	<i>Bombus</i>	<i>Andrena</i> , <i>Apis</i>
Fruit set	100%	64%		97%
Seed set	15–63%	40–75%		59–70%

evaluate the overall pollination level; however, our results indicate that, at least in certain years, between-individual differences in floral morphology cause significant differences in pollen receipt and thus in fecundity.

In conclusion, the floral traits of *E. dens-canis* vary in parallel (i.e. all floral parts are large, or all small), and have clear effects on fecundity. Within-population covariation in morphological traits has been attributed to two types of effect: selection effects (selective correlation), and genetic correlation (pleiotropy and/or linkage disequilibrium). Selective correlation occurs when certain combinations of traits increase fitness; genetic correlation refers to the existence of correlations regardless of the fitness effects of the resulting phenotypes (though see Armbruster 1996). Evaluation of the extent to which these factors influence variation in the morphology of *E. dens-canis* flowers is outside the scope of the present study. However, our results indicate that differences in floral morphology in this species lead to differences in female fecundity. The evolutionary consequences of these effects will largely depend on their constancy over time and their importance relative to other factors responsible for fitness differences between individuals (Herrera 1993, 1996).

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