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MUTUALISTS AND ANTAGONISTS MEDIATE FREQUENCY-DEPENDENT SELECTION ON FLORAL DISPLAY

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Abstract. Theory predicts that, with conflicting selection pressures mediated by mutualists and antagonists, alternative reproductive strategies can be maintained by negative frequency-dependent selection if it results in rare-morph advantage. We combined field experiments and surveys of natural populations to determine whether selection on floral display is frequency dependent in the self-incompatible herb *Primula farinosa*, which is polymorphic for inflorescence height and occurs in a short-scaped and a long-scaped morph. Among short-scaped plants, both pollination success, quantified as initiation of fruits and seeds, and seed predation were positively correlated with the relative frequency of the long-scaped morph. The relative strength of these effects and the direction of the resulting frequency-dependent selection on scape morph varied among years and populations. The results suggest that both mutualists and antagonists may mediate frequency-dependent selection and that frequency dependence may vary from positive to negative with rare-morph advantage, depending on the relative strength of these interactions.

Key words: alternative reproductive strategies; facilitation; floral display; frequency-dependent selection; genetic diversity; pollination; positive interactions; predation; Primula farinosa; Sweden.

INTRODUCTION

Mechanisms underlying frequency-dependent selection are of considerable interest because of their potentially strong influence on the evolutionary trajectories of local populations and genetic diversity (Hedrick 2006, Sinervo and Calsbeek 2006). Positive frequency-dependent selection and common-morph advantage should lead to monomorphism, while negative frequency-dependent selection may result in rare-morph advantage and stable polymorphism (Clark and O'Donald 1964). Under negative frequency-dependent selection, the predicted evolutionary stable-state frequency is defined by the intersection of the fitness functions of the different morphs (Gross 1996). The importance of negative frequency-dependent selection for the maintenance of genetic variation has been explored for several traits, including courtship and foraging behavior in *Drosophila* (Ayala and Campbell 1974, Fitzpatrick et al. 2007), color morphs in lizards and plants (Sinervo and Lively 1996, Gigord et al. 2001), and cytoplasmic male sterility factors in gynodioecious plants (McCauley et al. 2000, Städler and Delph 2002).

Theory predicts that both mutualistic and antagonistic interactions can result in frequency-dependent selection on traits affecting mating success (Gross 1996, Brockmann 2001). In a species dimorphic for a display trait, the probability that an inconspicuous morph is detected by an interactor can be expected to increase with the local frequency of the conspicuous morph. If the fitness of the inconspicuous morph is limited by the intensity of the mutualistic interaction, this may lead to negative frequency-dependent selection. For example, inconspicuous individuals may benefit from the presence of conspicuous individuals that attract pollinators or mates. On the other hand, if variation in fitness is mainly governed by an antagonistic interaction, this may result in positive frequency-dependent selection. For example, the fitness of inconspicuous individuals may be negatively affected by the presence of conspicuous individuals that attract enemies. Because the relative strength of mutualistic and antagonistic interactions may vary spatially and temporally, so may their joint effect on selection on display. However, empirical studies linking frequency-dependent selection and multispecies interactions are still few (Sinervo and Calsbeek 2006).

Reproductive strategies and traits that increase attractiveness to mutualists and mates but also increase the risk of predation and parasitism are common in both plants and animals. In plants, stature, the number, size, and arrangements of flowers, and nectar production can influence attractiveness to pollinators and pollination success (O'Connell and Johnston 1998, Chittka and Thomson 2001, Fenster et al. 2004, Bronstein et al. 2006), but also the risk of predation (Galen and Cuba 2001, Adler and Bronstein 2004, Cariveau et al. 2004, Strauss and Irwin 2004) and fungal parasitism (Collin et al. 2002, Giles et al. 2006). In animals, attractive appearance and behavior that enhance mating success

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may similarly be associated with a cost due to increased predation risk (Magnhagen 1991, Zuk and Kolluru 1998, Boyko et al. 2004) or susceptibility to sexually transmitted diseases (Boots and Knell 2002). Facilitation and competition between species mediated by mutualists and antagonists have received considerable attention (e.g., Callaway 1995, Palmer et al. 2003, Schmitt and Holbrook 2003, Morris et al. 2007). However, little is known about the extent to which mutualists and antagonists jointly affect the character and strength of frequency-dependent selection in populations polymorphic for display traits (Sinervo and Calsbeek 2006). If the net effect of multispecies interactions is negative frequency-dependent selection on display and rare-morph advantage, this should contribute to the maintenance of polymorphism within populations. However, if the net effect is frequency-independent or positive frequency-dependent selection on display, this should reduce the likelihood that polymorphism is maintained.

Here, we present a field-based study of multispecies interactions conducted over two years, which documents frequency-dependent selection on floral display mediated by both mutualists and antagonists. We studied the self-incompatible perennial herb *Primula farinosa*, which is dimorphic for floral display. It occurs either in a conspicuous long-scaped morph, with the flowers presented well above the soil surface, or in a markedly less conspicuous short-scaped morph, with the flowers presented very close to the ground. Short-scaped plants are often hidden by surrounding vegetation, and the difference in floral display affects interactions with pollinators, seed predators, and grazers. The short-scaped morph is more strongly pollen-limited than the long-scaped morph, but also subject to less intense seed predation and grazing (Ehrlén et al. 2002, Ågren et al. 2006, Vanhoenacker et al. 2006). Because scape morph influences mutualistic and antagonistic interactions associated with reproduction, the morphs can be regarded as two alternative reproductive strategies. In a previous experiment, we showed that the short-scaped morph produces fewer seeds when growing in monomorphic patches than when growing together with the long-scaped morph (Toräng et al. 2006). Here we examined the relationships between local morph ratio and fruit and seed production in the long-scaped and short-scaped morphs in experimental arrays and natural populations across a wide range of morph frequencies. We tested the predictions that (1) fruit initiation and seed set of both scape morphs increase with the local relative frequency of the conspicuous long-scaped morph, (2) damage from seed predators increase with the relative frequency of the conspicuous morph and counteract the facilitation of pollination, (3) the net effect of local scape morph frequency on seed output depends on the overall level of seed initiation and seed predation and therefore varies among populations and years, and (4) effects of the local morph frequency on reproductive success are stronger in the inconspicuous

short-scaped morph than in the conspicuous long-scaped morph and therefore result in frequency-dependent selection on scape morph.

METHODS

Study species

Bird's-eye primrose (*Primula farinosa* L., Primulaceae) is a hermaphroditic, self-incompatible, distylous perennial herb (Hambler and Dixon 2003). It produces a basal leaf rosette, and the flowers are arranged in an umbel. On the islands Öland and Gotland, off the southeast Swedish coast, it occurs as two distinct scape morphs (Lagerberg 1948). Individual plants produce either a regular 2–25 cm long scape, with the flowers presented well above the soil surface, or a 0–6 cm short scape, with the flowers presented very close to the ground. Scape morphs overlapping in height can be distinguished by the appearance of the scape; long scapes are thin and smooth, whereas short scapes are markedly thicker and striate. The relative frequency of the short-scaped morph varies from 0% to 67% among natural populations ($N = 52$ populations on Öland in 2001; J. Ågren and J. Ehrlén, *unpublished data*) and even more among patches within populations (J. Ågren, J. Ehrlén, P. Toräng, and D. Vanhoenacker, *personal observations*). Controlled crosses suggest that scape morph is determined by a single locus with a dominant allele for short scape (J. Ågren and J. Ehrlén, *unpublished data*). Like many other *Primula* species, *P. farinosa* is distylous, and populations thus include both long-styled (pin) and short-styled (thrum) plants. Scape morph is not correlated with style morph (see *Results: Natural populations*). *Primula farinosa* grows in moist meadow vegetation on calcareous ground, and its persistence at a given site is favored by grazing (Sterner 1986, Lindborg and Ehrlén 2002). Flowering takes place in May. In the study area, butterflies (especially *Pyrgus malvae*) and solitary bees (especially *Osmia bicolor*) are the main pollinators. Foraging pollinators frequently move between scape morphs (J. Ågren, J. Ehrlén, P. Toräng, and D. Vanhoenacker, *unpublished data*), suggesting that mating is not assortative. Flight distances are typically shorter than 1 m. The fruit is a multi-seeded capsule, which matures in July. Initiated fruits are sometimes attacked by larvae of the tortricid moth, *Falseuncaria ruficiliana*, but the intensity of seed predation varies among populations and years, from zero to >70% of fruits produced by long-scaped plants attacked in individual populations ($N = 45$ populations in 2000, 52 populations in 2001; J. Ågren and J. Ehrlén, *unpublished data*). In attacked plants, most seeds are consumed by the developing larvae. The entire inflorescence is sometimes eaten by domesticated grazers (cattle, sheep, and horses).

Experimental arrays

To examine the effect of scape morph ratio on fruit initiation, seed set, and seed predation, we established 44

experimental arrays of plants in 2005 and 54 experimental arrays in 2006, consisting of a total of 352 and 432 plants, respectively. In early May, plants were dug up from a meadow (Amossen, 56°50′ N, 16°50′ E) on Öland and kept in pots. When the plants began to flower, they were allocated to one of the experimental arrays. Arrays were distributed randomly at nodes in a rectangular grid containing 100 nodes separated by 30 m in the meadow of origin. Inflorescences produced by *P. farinosa* individuals that grew in the area but that were not included in the experiment were cut off. In 2005, each array consisted of eight plants of which zero (0%), two (25%), four (50%), or six (75%) were long-scaped. In 2006, we also included arrays of the same size in which one (12.5%) or eight (100%) of the plants were long-scaped. Experimental plants were separated by 0.3 m and ordered in a rectangular array in which scape morphs were systematically interspersed so that the rare morph always had the common morph as its closest neighbors. The scape was 1.3 ± 1.7 cm long (mean ± SD; range 0.0–4.7 cm, $N = 430$) in the short-scaped morph and 9.1 ± 3.0 cm long (range 5.0–20 cm, $N = 235$) in the long-scaped morph. The style morph ratio was kept even among both short-scaped and long-scaped plants in all arrays except for the treatment with only one long-scaped plant. In the latter treatment, style morph of the long-scaped plant was randomly assigned and the style morph ratio among the short-scaped plants was adjusted to yield an overall even style morph ratio in the array. Arrays mimicked the size and density of small patches within natural populations of *P. farinosa*. Each scape morph ratio treatment was replicated 11 times in 2005 and 9 times in 2006. During flowering, we recorded the number of flowers produced by each plant. Flower production did not vary among treatments (ANOVA based on array means, $F_{3,39} = 1.42$, $P = 0.25$ in 2005 and $F_{5,47} = 0.52$, $P = 0.76$ in 2006) or scape morphs (*t* test based on array means, $t_{72} = 0.637$, $P = 0.53$ in 2005 and $t_{83} = 0.635$, $P = 0.63$ in 2006). Moreover, a two-way ANOVA indicated no statistically significant effect of treatment, scape morph, or their interaction on flower production in polymorphic populations ($P > 0.1$ in all cases). Height of the surrounding vegetation did not vary among treatments (8.3 ± 2.1 cm in 2005 and 7.2 ± 1.9 cm in 2006) and were not included in analyses. In 2005, 30 plants and in 2006, 83 plants were damaged by drought, grazing, or trampling by cattle and sheep and were removed from further analyses. As is generally observed, the long-scaped morph was more frequently damaged by grazers than the short-scaped morph. However, the proportion of long-scaped plants that was grazed did not vary among treatments ($\chi^2 = 6.4$, df = 4, $P > 0.1$), and grazing damage to short-scaped plants was very low. Moreover, because the plants were grazed after flowering, the scape morph ratio among flowering plants was not affected. We excluded the effect of grazing, because we here focus on frequency-dependent interactions with pollinators and seed predators. The

intensity of grazing varies considerably among populations and among years (from 0% to 91% of long-scaped plants grazed in individual populations; $N = 45$ populations in 2000, 52 populations in 2001; J. Ågren and J. Ehrlén, *unpublished data*), and it was not logistically possible to include grazing intensity as an additional factor in the experiment.

To explore the effect of scape morph ratio on measures of female reproductive success, we used linear regression models for each scape morph to examine the effect of the proportion of long-scaped plants on mean fruit initiation (i.e., the proportion of flowers initiating fruits), fruit survival (1 – the proportion of initiated fruits that was damaged by seed predators), fruit production per plant, seed set (i.e., the proportion ovules developed into seeds), and mean number of mature seeds per plant. Analyses were conducted on mean values per scape morph and array. Number of flowers, fruits, and seeds per plant were log-transformed, and fruit initiation, proportion of surviving fruits, and seed set were arcsine square-root transformed prior to analysis. Variances in the response variables were equal among treatment categories within scape morphs, but the variance in mean number of mature seeds per plant was higher in the long-scaped than in the short-scaped morph (Levene's test = 4.2, $P = 0.04$ for seed production; $P > 0.05$ in all other cases). The proportion of initiated seeds that aborted was very low, and this component of female reproductive success was not analyzed further. In 2005, the proportion of initiated seeds that aborted ranged from 0.03 to 0.05 (treatment means), while in 2006 no initiated seeds aborted.

For the polymorphic arrays, we examined how scape morph frequency affected selection on scape length through female function by documenting the relationship between relative reproductive success of the short-scaped morph and the proportion of short-scaped plants, using linear regression. For each array, relative reproductive success of the short-scaped morph was calculated as $RR_{short} = \log_e$(mean reproductive success of the short-scaped morph/mean reproductive success of the long-scaped morph). With this measure, a value of zero represents equal reproductive success of the two scape morphs. Relative reproductive success was calculated based on fruit initiation, fruit survival, fruit production per plant, seed set, and number of mature seeds per plant. In one treatment (12.5% long-scaped plants), a single long-scaped plant was scored in each array. This resulted in a particularly high variance in total seed production per plant and some arrays for which it was not possible to estimate relative reproductive success because all seeds produced by the single plant were consumed by the seed predator. For calculation of RR_{short} in arrays with a single long-scaped plant, we therefore used mean seed production over all those arrays as an estimate of the reproductive success of the long-scaped morph.

Natural populations

To determine whether effects observed in experimental arrays could be detected also in natural populations, we examined the relationship between local scape morph ratio and plant reproductive success. In 2005, short-scaped plants were examined in three populations ($N = 55$–177 plants per population; Appendix). In 2006, we examined the relationships between local morph ratio and reproductive success of both short- and long-scaped plants in three populations of which one population was examined also in 2005 ($N = 68$–90 per morph and population; Appendix). Focal plants were chosen haphazardly throughout the population with the restriction that they should be separated by >80 cm. During flowering, we recorded the total number of flowers produced and the style morph of focal plants. Neighboring conspecific plants within a radius of 40 cm were classified according to scape morph (short vs. long) and style morph (same as the focal plant vs. different). We thus determined the floral neighborhood within an area of similar size as the experimental arrays. For each focal plant, we recorded the number of initiated, damaged, and mature fruits and the number of mature seeds. Among focal plants, scape morph was not associated with style morph in any population (χ^2 test, $P > 0.2$ in all cases).

For each population and year, we used multiple regression to examine how fruit and seed production of focal short-scaped and long-scaped plants were related to the number of flowers produced by the focal plant, the number of neighbors, the proportion of long-scaped neighbors, and the proportion of plants of the other style morph. The effect of number of neighbors was not statistically significant in any case ($P > 0.1$) and was removed from the final models. In the natural populations, damage from seed predators was low in 2005, and analyses of fruit initiation gave the same results as analyses of fruit production (data not shown). In 2006, when damage was more common, we report the effects on fruit initiation and survival. Grazing damage was not frequent.

Number of neighbors, flowers, fruits, and seeds were log-transformed and fruit initiation and survival were arcsine square-root transformed prior to analyses. For focal plants both in experimental arrays and in natural populations, we initially examined effects of style morph in all analyses. No effect of style morph was found ($P > 0.1$ in all cases) and we therefore present only models without style morph. Statistical analyses were performed in R version 2.4.1 (R Development Core Team 2006).

RESULTS

Experimental arrays

Overall, long-scaped plants initiated more fruits, but the proportion of fruits escaping damage by the seed predator, the tortricid moth *Falseuncaria ruficiliana*, was lower among long-scaped than among short-scaped plants. In 2005, fruit initiation was 96% ± 1.0% (mean ± SE, $N = 116$ plants) among long-scaped plants and 72% ± 2.0% ($N = 206$ plants) among short-scaped plants. In 2006, fruit initiation was 91% ± 2.9% ($N = 124$ plants) among long-scaped plants and 43% ± 3.9% ($N = 225$ plants) among short-scaped plants. In 2005, fruit survival was 25% ± 3.8% ($N = 116$ plants) among long-scaped plants and 75% ± 2.8% ($N = 192$ plants) among short-scaped plants. In 2006, fruit survival was 37% ± 4.0% ($N = 122$ plants) among long-scaped plants and 91% ± 2.1% ($N = 148$ plants) among short-scaped plants.

Among short-scaped plants, both fruit and seed initiation and damage from seed predators increased with the proportion of the long-scaped morph. The relative strength of these effects and therefore their net effect on the relationship between scape morph ratio and seed production of short-scaped plants varied among years. In the short-scaped morph, fruit initiation increased, but the proportion of surviving fruits decreased with increasing proportion of long-scaped plants in 2005 (Fig. 1). Because the increase in fruit initiation did not balance the decrease in survival in 2005, total fruit production of the short-scaped morph decreased with increasing proportion of long-scaped plants. The number of seeds initiated per ovule increased with increasing frequency of the long-scaped morph in 2005. As a result, total seed production of short-scaped plants was not correlated with the frequency of the long-scaped morph this year. Also in 2006, fruit initiation increased with increasing proportion of long-scaped plants. In this year seed predation among short-scaped plants was less intense than the year before (ANOVA, $F_{1,69} = 12.5$, $P < 0.001$) and not related to the scape morph ratio in the array (Fig. 1). The number of seeds initiated per ovule was not related to frequency of the long-scaped morph in 2006. As a result, both fruit and seed production among short-scaped plants increased with increasing frequency of the long-scaped morph in 2006.

Among long-scaped plants only the number of seeds per ovule in 2006 (linear regression, $b = 0.37$, $R^2 = 0.14$, $P < 0.05$) increased with the frequency of the long-scaped morph ($P > 0.1$ for fruit initiation, fruit survival, number of fruits, and number of seeds per plant in 2006 and for all response variables in 2005).

In polymorphic arrays, the relative seed output of the short-scaped morph increased with increasing frequency of long-scaped plants in 2006 (Fig. 2). In 2006, relative fruit initiation (linear regression, $b = 0.79$, $R^2 = 0.27$, $P < 0.01$), relative fruit production (linear regression, $b = 1.98$, $R^2 = 0.25$, $P < 0.01$), and seed production per plant (Fig. 2) were positively related to the frequency of long-scaped plants. The model indicated that relative seed output per plant, quantified as $\log_e$(mean number of seeds produced by the short-scaped morph/mean number of seeds produced by the long-scaped morph), would be zero, i.e., short- and long-scaped plants would produce equal numbers of seeds in arrays consisting of 41% long-scaped plants (Fig. 2). In 2005, the relative reproductive success of the two scape morphs was independent of frequency, and mean seed output was
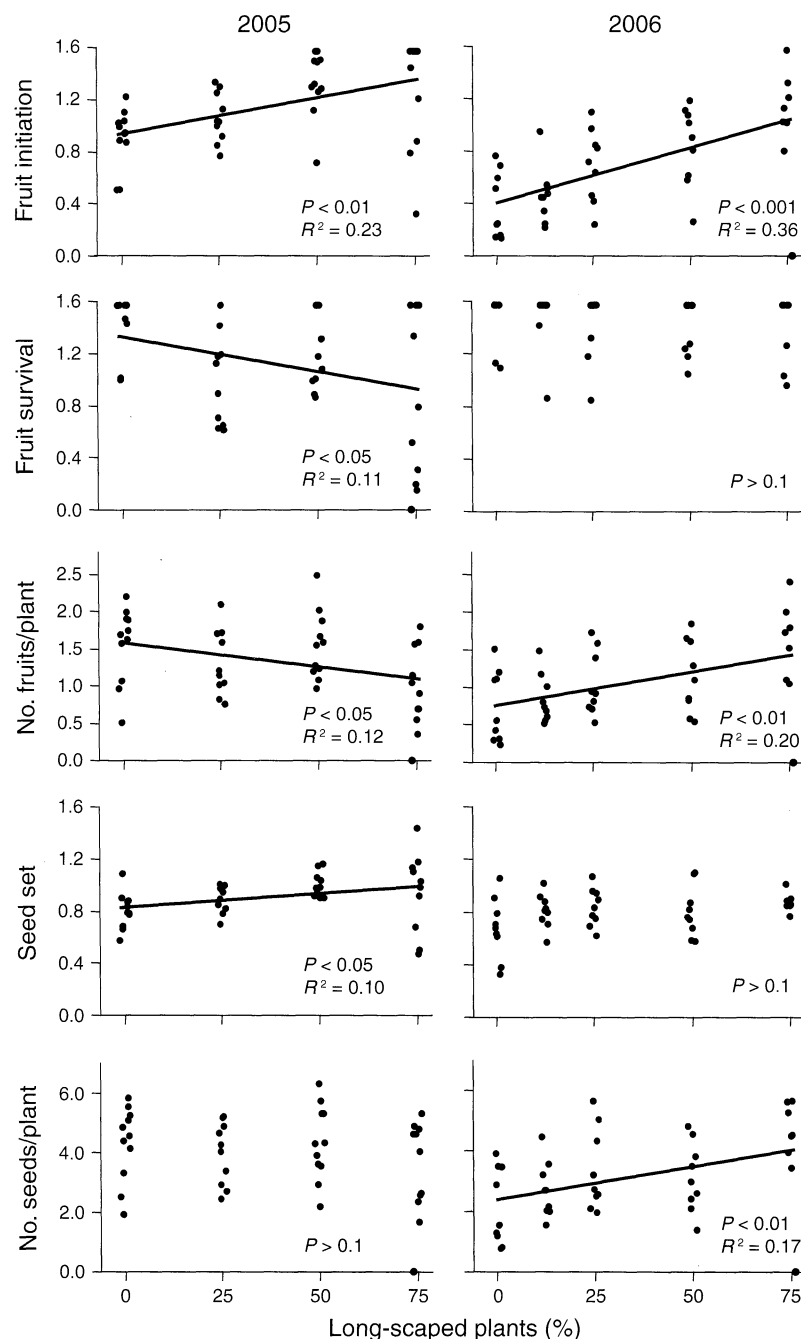
FIG. 1. Fruit initiation, surviving fruits, number of fruits per plant, seed set (proportion of ovules developing into mature seeds), and number of seeds per plant of short-scaped *Primula farinosa* as a function of scape morph ratio in field experiments conducted on Öland, Sweden, in 2005 and 2006. *P* and R^2 values from linear regression analyses are indicated. Fruit initiation, survival, and seed set were arcsine square-root transformed (originally measured as proportions), and number of fruits and seeds were $\log_e$-transformed prior to analyses. The plots depict mean values per array.

greater among short-scaped plants than among long-scaped plants (data not shown).

Natural populations

The association between local scape morph ratio and components of female reproductive success (fruit initi-

ation, fruit and seed production) varied among natural populations and years, as did the proportion of fruits attacked by seed predators (Appendix). In 2005, seed production among focal short-scaped plants increased with the frequency of the long-scaped morph in the Möckelmossen and Mörbylilla 2 populations, but not in
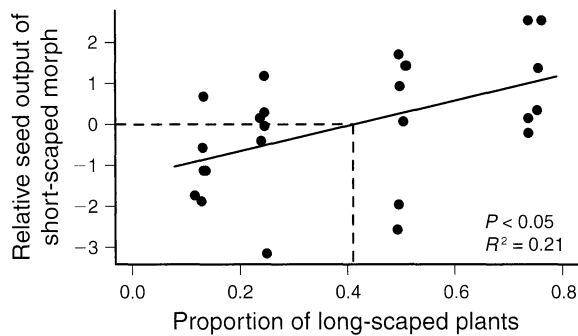
FIG. 2. Relative seed output of short-scaped *Primula farinosa* ($\log_e$[mean number of seeds produced by short-scaped morph/mean number of seeds produced by long-scaped morph]) as a function of scape morph ratio in a field experiment on Öland, Sweden, in 2006. P and R^2 values from linear regression analysis are indicated. Dashed lines indicate the scape morph ratio at which short-scaped and long-scaped plants are predicted to produce equal numbers of seeds.

the Mörbylilla 1 population (Table 1, Fig. 3). In this year, fruit predation was very low and both fruit initiation and fruit production of the short-scaped morph increased with the local frequency of the long-scaped morph in the Möckelmossen population (Table 1, Fig. 3). In 2006, a large proportion (28–55%) of short-scaped plants did not initiate fruits, and we found no relationship between fruit initiation, fruit survival, fruit production, or seed production of focal short-scaped plants and local scape morph ratio or other measured explanatory variables using linear regression ($P > 0.1$ in all cases). Among long-scaped focal plants, fruit initiation, fruit survival, and seed production were not significantly correlated with the local frequency of the long-scaped morph in any population ($P > 0.05$).

DISCUSSION

This study has demonstrated that both mutualistic and antagonistic interactions can result in frequency-dependent selection on floral display. The results suggest that interactions with mutualists can lead to negative frequency-dependent selection on display traits, while

interactions with antagonists may lead to positive frequency dependence. The net effect of scape morph ratio on fitness should depend on the relative strengths of these interactions, which may vary both among populations and among years. In *Primula farinosa*, fruit and seed initiation of the inconspicuous short-scaped morph increased with the frequency of the conspicuous long-scaped morph, but so did fruit mortality due to damage from the predispersal seed predator. In one of the two years, variation in fruit initiation resulted in negative frequency-dependent selection on scape morph and rare-morph advantage. However, in the other year the effects of frequency-dependent fruit initiation and seed predation in the short-scaped morph balanced and selection on scape morph was not frequency dependent.

The results support the notion that the character and intensity of frequency-dependent selection on display is influenced by both mutualistic and antagonistic interactions. The negative frequency-dependent selection on scape morph was caused by variation in fruit and seed initiation and therefore most likely the effect of interactions with pollinators. Fruit initiation and seed set are more strongly pollen-limited in short-scaped than in long-scaped *P. farinosa* (Ehrlén et al. 2002, Ågren et al. 2006, Vanhoenacker et al. 2006). In the present study, seed abortion was very low and did not vary between scape morphs or scape morph ratio treatments. The low seed abortion suggests that plants were pollen-limited rather than resource-limited and that variation in fruit and seed initiation reflected differences in pollination intensity. Our results are consistent with the idea that long plants may act as beacons that attract pollinators and thus facilitate the pollination of the short-scaped morph (Toräng et al. 2006). This mechanism may lead to negative frequency-dependent selection on scape morph, as suggested by the results from the field experiment in 2006.

Our results demonstrate that antagonists can counteract facilitation provided by conspicuous neighbors and suggest that the strength and direction of frequency-dependent selection on display should depend on the abundance and selectivity of both mutualists and

TABLE 1. The effects of local scape morph ratio, proportion of plants of the other style morph, and number of flowers (log-transformed) on fruit and seed production (both log-transformed) of short-scaped plants in three populations of *Primula farinosa* on Öland, Sweden, in 2005, analyzed with multiple regression.

Source of variation	Möckelmossen		Mörbylilla 1		Mörbylilla 2	
	b	$t_{3, 173}$	b	$t_{3, 51}$	b	$t_{3, 78}$
Fruit production						
Frequency of the long-scaped morph	0.302	2.37*	−0.266	−1.03	0.379	1.57
Frequency of the other style morph	−0.117	−0.864	0.224	1.01	0.237	1.22
No. flowers	0.608	6.70***	0.929	7.24***	1.08	5.99***
Seed production						
Frequency of the long-scaped morph	0.666	1.81†	−0.560	−0.763	1.44	2.01*
Frequency of the other style morph	−0.0199	−0.0507	0.117	0.184	1.10	1.89
No. flowers	1.30	4.91***	2.35	6.44***	1.82	3.38**

Notes: Partial regression coefficients (b) and their associated t values are given. The regression coefficients are not standardized.
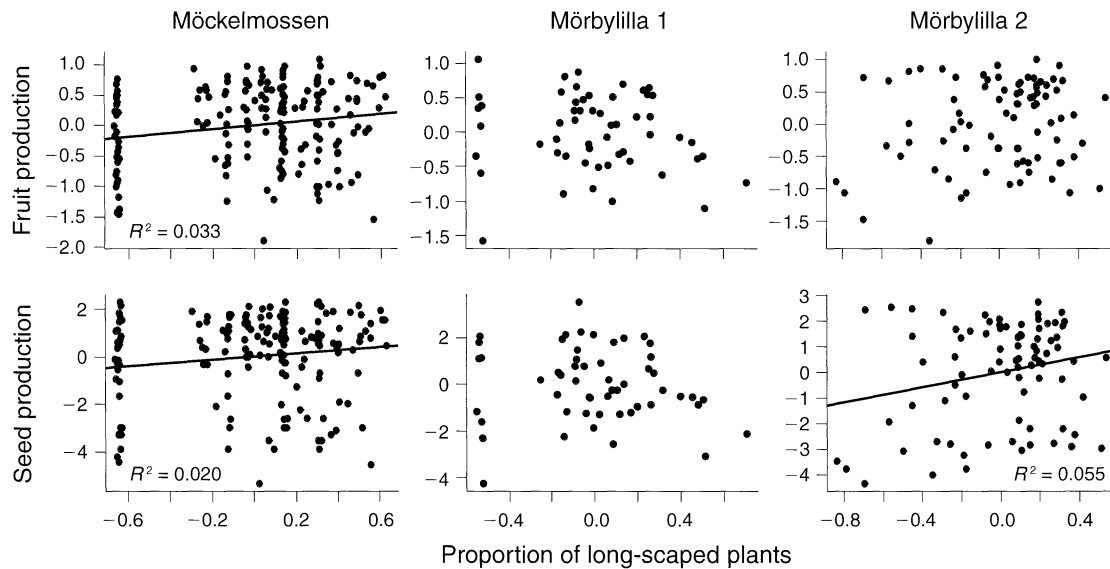† $P < 0.08$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

FIG. 3. Added-variable plots illustrating the relationship between local scape morph ratio and number of fruits and number of seeds produced by short-scaped *Primula farinosa* in three populations on Öland, Sweden, in 2005. The plots depict fruit production (top panels) and seed production (bottom panels) as a function of the proportion of the long-scaped morph among conspecific plants within 40 cm of the focal plant when the effects of the number of flowers of the focal plant and the proportion of plants of the other style morph are accounted for.

antagonists. For short-scaped plants in the experimental arrays, the proportion of fruits surviving predispersal seed predation was negatively related to the frequency of the long-scaped morph in 2005. This suggests that seed predators are attracted to plants by the same cues as pollinators and show that fruit survival may be positively frequency dependent among short-scaped plants. In experimental arrays in 2005, effects of morph frequency on fruit initiation and seed predation balanced one another, and seed production of short-scaped plants was not correlated with the frequency of the long-scaped morph. In 2006 seed predation was less intense and the positive effect of long-scaped neighbors on fruit initiation was not balanced by a higher seed predation, and fruit and seed production of short-scaped plants were positively related to the frequency of the long-scaped morph (negative frequency dependence).

Frequency-dependent selection may reflect frequency-dependent performance of one or both morphs in dimorphic populations (Gross 1996). In *P. farinosa*, the seed output of the short-scaped morph, but not of the long-scaped morph, was affected by the local morph ratio. Apparently, female reproductive success is more susceptible to context in the short-scaped morph than in the long-scaped morph, and frequency-dependent selection on scape morph was driven by context-dependent fitness variation among short-scaped plants.

Our surveys in natural populations suggest that the frequency-dependent selection demonstrated in experiments can be detected also in natural populations of *P. farinosa*. In natural populations, fruit initiation, number of intact mature fruits, and seed production of short-

scaped plants increased with increasing frequency of the long-scaped morph among neighbors in two of three populations in 2005, results that are in accordance with the patterns seen in the experimental arrays in 2006. The results indicate that interactions with pollinators may result in negative frequency-dependent selection on scape morph when antagonists are rare, as in the 2006 experimental and 2005 natural populations, but that in other years antagonists may reverse the direction of frequency-dependent selection on scape morph. The results suggest that the combination of variation in interaction intensity with mutualists and antagonists and frequency-dependent selection on floral display results in spatiotemporal variation in selection on floral display. This should contribute to the observed variation in scape morph frequencies among natural populations and the long-term maintenance of the two scape morphs.

Grazing can markedly affect the relative fitness of long- and short-scaped *P. farinosa*, but is not expected to affect the slope of the relationship between scape morph ratio and morph-specific fitness measures. Long-scaped plants are more frequently damaged by grazers than short-scaped plants. In a population subject to negative frequency-dependent selection, long- and short-scaped plants should therefore have equal fitness at a higher frequency of the short-scaped morph in the presence than in the absence of grazers. Because *P. farinosa* is not a food item particularly sought after by the grazers, grazing is not likely to be frequency dependent. Consistent with this prediction, grazing damage was not related to morph ratio in the array experiment. In a

long-term experiment, we currently examine the direct and indirect effects of ungulate grazing on interactions with pollinators and seed predators and on the dynamics and scape morph composition of *P. farinosa* populations.

Models of stable coexistence of alternative reproductive strategies assume divergent selection or that the fitness of at least one of the strategies is negatively frequency dependent and that the fitness functions of the two strategies intersect to produce a rare-morph advantage (Gross 1996, Brockmann 2001). Negative frequency-dependent selection mediated by pollinators should contribute to the maintenance of the striking scape length dimorphism in *P. farinosa* in the study area, where scape morph frequencies vary considerably both within and among populations. Frequency-dependent selection caused by behavioral preferences of mutualists is well known from plant–pollinator systems in which pollinator preferences are expected to lead to positive frequency-dependent selection on floral display and monomorphism in rewarding species (e.g., Smithson and Macnair 1996). Negative frequency-dependent selection due to variation in pollination success is thought to contribute to the maintenance of flower color polymorphism in the rewardless orchid *Dactylorhiza sambucina* (Gigord et al. 2001) and in the rewarding *Clarkia xantiana* subsp. *xantiana*, which is pollinated by several specialist bee species (Eckhart et al. 2006), and of intermediate sex ratios in gynodioecious *Silene vulgaris* (McCauley et al. 2000). Frequency-dependent selection caused by behavioral preferences of antagonists is best known from predator–prey systems, in which predator preference for the commonest prey can lead to a rare-morph advantage and hence negative frequency-dependent selection and polymorphism (Allen 1988, Olendorf et al. 2006). This is the first study to report frequency-dependent selection on plant stature. Regression models indicated that under the conditions prevailing in the experimental arrays in 2006, short- and long-scaped plants would produce equal numbers of seeds in arrays consisting of 41% long-scaped plants.

To conclude, the present study has shown that frequency-dependent selection may be mediated by both mutualists and antagonists responding to the same trait and that frequency dependence may vary from positive to negative with rare-morph advantage depending on the relative strength of these interactions. In recent years there has been an increasing awareness that community context can affect the direction and strength of selection (Johnson and Stinchcombe 2007). The results of this study illustrate the manner in which the genetic structure of a population can influence the effects of mutualistic and antagonistic interactions on trait selection. They make clear that an understanding of local selection, as well as geographic selection mosaics, may require that both population composition and community context are considered.

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APPENDIX

Statistics from the large natural populations examined (*Ecological Archives* E089-093-A1).