

Cost and benefits of attractive floral traits in the annual species *Madia sativa* (Asteraceae)

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Abstract The maintenance of flower size variation within populations might be explained by conflicting selection pressures on floral traits that may involve biological agents, such as mutualists and antagonists, and allocation costs associated with floral display. The annual species *Madia sativa* (Asteraceae) exhibits ample variation in the number of ray florets in natural populations. This field study aimed at evaluating the costs and benefits associated with floral traits in *M. sativa*. In particular, we addressed two main questions: (1) Is the number of ray florets positively associated with pollinator visitation rate? (2) Is there a fitness cost of ray floret maintenance when pollinators are absent? We detected one benefit of conspicuous ray capitula: a strong preference by insect pollinators. We also confirmed the occurrence of costs: when pollinators were excluded conspicuous ray capitula had a reduced reproductive assurance via autogamous selfing, and there were trade-offs between the number of ray florets and seed mass and seed germination. Results suggest that the maintenance of within-population variation in the number of ray florets in *M. sativa* is explained, at least in part, by the balance between costs and benefits associated with this floral trait.

Keywords Floral trait polymorphism · Germination · Pollinator preference · Ray florets · Reproductive assurance · Seed mass · Selfing

Introduction

There is considerable evidence that dense patches, taller plants, extensive floral display, conspicuous flowers and large corolla sizes may increase pollinator attraction (Cruzan et al. 1988, Galen 1989, Young and Stanton 1990, Eckhart 1991, Galloway et al. 2002). Various studies have reported positive directional selection on flower size (Galen and Newport 1987, Galen 1989, Campbell 1991, Herrera 1993,

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Conner and Rush 1996). However, small flowers yet persist, and natural plant populations exhibit broad variation in flower size. The maintenance of flower size variation within populations might be explained by conflicting selection pressures on floral traits (Galen 1999). This may involve biological agents such as pollinators, nectar robbers, flower herbivores and seed predators, and allocation costs associated with floral display (Brody 1992, Galen 1999, Andersson 2001, 2005, Fenner et al. 2002, Cariveau et al. 2004). Allocation costs result from resource investment in the production and maintenance of attractive floral structures, which may reduce the amount of available resources for fruit production (Ashman and Schoen 1997). For instance, Andersson (1999, 2000, 2005) found that petals in two species of *Nigella* (Ranunculaceae) and ray florets in *Achillea ptarmica* (Asteraceae) entail a cost in terms of fruit set, seed quality and seed germination.

In Asteraceae the basic attraction unit for pollinators is the inflorescence (capitulum) composed of ray florets, which are petal analogues (Mani and Saravanan 1999). The presence of ray florets is positively associated with plant fitness when pollinators are abundant (Stuessy et al. 1986, Nielsen et al. 2002). However, the abundance and visitation rates of pollinators can vary markedly among and within years. Therefore, the maintenance of floral traits related to attractiveness (e.g., number of ray florets) might involve a cost, expressed as a reduction in plant fitness when the abundance and/or activity of pollinators are low. The interplay of costs and benefits of attractive floral traits, whose outcome depends on the relative abundance/visitation rate of pollinators, might partly explain the persistence of within-population variation in floral phenotype. Although several studies have addressed the trade-off involved in selection on floral traits (pollinator preference versus cost of reproduction), fewer studies have employed an experimental approach including pollinator exclusion, measurement of floral traits and assessment of fitness components.

The annual species *Madia sativa* (Asteraceae) is self-compatible and partially autogamous (Arroyo and Uslar 1993), but it is unknown whether pollinator presence enhances fruit production. This species exhibits ample variation in the number of ray florets in natural populations (Fig. 1). The present field study aimed at evaluating the costs and benefits associated with attractive floral traits in *M. sativa*. In particular, we addressed two main questions: (1) Is the number of ray florets positively associated with pollinator visitation rate? (2) Is there a fitness cost of ray floret maintenance when pollinators are absent? We also assessed plant density, plant height, and floral display because these variables could also affect pollinator attraction.

Materials and methods

Study site

This study was conducted at 2400 m altitude in the Andes of central Chile (33°21' S; 70°17' W). The climate is alpine with Mediterranean influence, with a mean annual precipitation of 431 mm, falling predominantly as snow during the winter (June–August). The growing season at this altitude commonly extends from October to May (Arroyo et al. 1981). Vegetation is dominated by small (<45 cm) spiny shrubs: *Berberis empetrifolia* (Berberidaceae), *Chuquiraga oppositifolia* (Asteraceae) and *Anarthrophyllum cumingii* (Cytiseae). Herbaceous species, such as *Madia sativa*

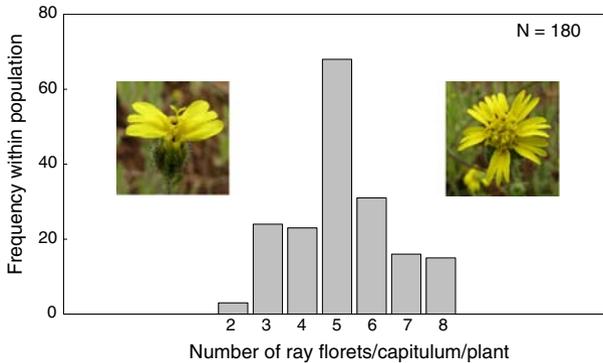


Fig. 1 Histogram showing the frequency of capitula with different number of ray florets in a population of *Madia sativa* (Asteraceae) from Central Chile

(Asteraceae), *Acaena pinnatifida* (Rosaceae), *Phacelia secunda* (Hydrophyllaceae), *Stachys philippiana* (Lamiaceae), and *Senecio* spp. (Asteraceae), are also abundant.

Plant species

Madia sativa (Mol) (Asteraceae) is an annual selfing plant species (Arroyo and Usler 1993). Plant height varies from 10 to 90 cm. The basal leaves form a rosette and upper leaves are opposite along the branches. Leaves and stems are covered by glandular and non-glandular trichomes. *M. sativa* has yellow rayed capitula with hermaphroditic disc florets and fertile female ray florets (Hoffmann 1998). The capitula (1.5–2 cm diameter) are located apically in main and secondary branches. Each plant produces numerous capitula (up to 100) over its 3–7 week flowering period, but they open gradually, each one lasting approximately 7 days.

Visitation of pollinators

In January 2005 we randomly established 12 plots of 3 × 3 m within a large *M. sativa* population located in a plateau. We calculated patch density (number of *M. sativa* plants per plot) and randomly marked 15 plants within each plot. In each tagged plant we measured the number of open capitula, number of ray florets per capitulum and plant height. We determined pollinator visitation rates and duration of pollinator visits. A pollinator visit was defined as the event in which an insect landed on at least one open capitulum of the plant and became covered with pollen. Pollinators that only flew above or around the plants and then left were not included in the analyses. We conducted observations during 4 h in each plot, from 9:00 to 13:00. Total observation time in the population was thus 48 h.

Plant fitness

To assess the fitness costs associated with ray florets in absence of pollinators, in January 2005 we randomly chose 36 plants from the study population. In each plant we tagged two buds located at similar height. Pollinators were excluded from one bud using a nylon mesh bag and the other bud served as control. At

the onset of anthesis we counted the number of ray florets in each tagged capitulum. At the end of anthesis capitula exposed to pollinators were bagged and two months later capitula from both treatments were collected. This experimental approach is protected against incidental variation that is not relevant to the hypothesis we want to test, i.e., it reduces the random error not related to treatment differences. Thus, the use of paired buds minimizes possible biases due to plant genotype, ontogeny or microenvironment. It is important to acknowledge that we assumed that imposing the treatment on one capitulum did not alter the result in the contiguous capitulum. Thus, we assumed that pollinators were neither attracted nor repelled by mesh bags, and that pollination of an open pollinated flower would not result in lowered seed production in the pollinator exclusion flower. We recorded in each capitulum the seed/floret ratio (a measure of success in flower-to-fruit conversion), seed mass and seed germination as fitness components. Seed/floret ratio was calculated as the number of seeds produced/total number of florets. We distinguished seeds produced by ray and disc florets, and all seeds were individually weighed. Seeds were then stratified at 4°C for 30 days and placed in a chamber at 25°C for 30 days to assess germination (Sierra-Almeida 2003).

Statistical procedures

We evaluated the relationship between pollinator visit and the number of ray florets. First, we run a multiple logistic regression to estimate the probability of pollinator visit to at least one capitulum using as predictor variables: number of ray florets per capitulum, number of open capitula and plant height of the focal plant, and patch density. For this purpose, we considered probability of pollinator visit as a dichotomous variable: plant visited at least once = 1; plant not visited = 0. Second, we also evaluated correlations among predictor variables and between predictors and the number of pollinator visits (Pearson product moment correlation).

In order to assess whether the number of ray florets affected the seed/floret ratio we used Analysis of Covariance (ANCOVA). The full model included pollinator exclusion as a fixed factor, the number of ray florets as covariate, and the interaction of factors ($N = 36$ plants). To increase the statistical power to detect effects of the pollination treatment, we pooled seeds produced by disc and ray florets to calculate seed/floret ratio. For seed mass we did discriminate between seeds from ray and disc florets to explore possible differences between the two types of florets (Imbert et al. 1996; Rocha 1996). Therefore, we used the same model but floret type was also included as fixed factor, and all interactions of factors were considered. Differences in the relationship between the number of ray florets and seed/floret ratio or seed mass in each pollination treatment were tested as significant statistical interactions (number of ray florets \times pollination treatment).

For germination, because we did not find differences between seed mass in disc and ray florets, we pooled seeds per capitulum and assessed germination percentage. We compared the germination percentage between pollinator treatments using a Wilcoxon matched pairs test ($N = 35$) because data showed a non-normal distribution. In addition, we calculated in each pollinator treatment the correlation (Spearman rank order correlations) between germination percentage and the number of ray florets and the mean seed mass per capitulum/plant.

Results

Preference of pollinators

Flowers of *Madia sativa* were visited by insects, mainly dipterans and hymenopterans. The most important pollinators were *Villa* sp. (Hym., Bombyliidae), *Scaeva* sp. (Dip., Syrphidae), *Leioproctus andinus* (Hym., Colletidae) and *Bombus dahlbomii* (Hym., Apidae) (data not shown). The number of ray florets, plant height and number of open capitula were positively correlated to the number of pollinator visits, and all three variables showed positive correlations among them (Table 1). Multiple logistic regression analysis (Table 2) revealed that the probability of pollinator visit increased significantly with number of ray florets, plant height (Fig. 2) and patch density. The number of open capitula did not influence the probability of pollinator visit (Table 2).

Seed/floret ratio

The number of ray florets did not affect the seed/floret ratio, but the pollinator treatment and the pollinator treatment \times number of ray florets interaction significantly affected the seed/floret ratio (Table 3). The mean seed/floret ratio was lower in capitula where pollinators were excluded (0.770 ± 0.032 ; Mean \pm SE) than in capitula exposed to pollinators (0.854 ± 0.023). We found a positive correlation between the number of female ray florets and the number of hermaphroditic disc florets. For excluded capitula: number of disc florets = $3.5 + 1.1 \times$ number of ray florets; $R^2 = 0.16$, $P < 0.001$. For exposed capitula: number of disc florets = $1.8 + 1.35 \times$ number of ray florets; $R^2 = 0.11$, $P < 0.001$. The mean number of hermaphroditic florets was similar in the pollinator exclusion and control treatments (t -test for dependent samples, $P = 0.33$). While in the control (pollinator exposed) treatment the number of ray florets was not correlated to seed/floret ratio (Pearson

Table 1 Correlation among number of ray florets, number of open inflorescences, plant height, patch density and number of pollinator visits in a *Madia sativa* population

	Number of open capitula	Plant height	Patch density	Number of visits
Number of ray florets	0.46**	0.68**	-0.13	0.46**
Number of open capitula		0.37**	0.12	0.39**
Plant height			-0.21*	0.53**
Patch density				0.036

Pearson product moment correlation; * $P < 0.05$; ** $P < 0.01$

Table 2 Relationship between the probability of pollinator visit (dependent variable) and the number of ray florets, number of open inflorescences, plant height and patch density. A multiple logistic regression was applied

	Estimate \pm SE	Wald	<i>P</i>
Number of ray florets	0.085 \pm 0.023	12.80	0.032
Number of open capitula	0.379 \pm 0.177	4.55	0.259
Plant height	5.390 \pm 1.038	26.97	0.0001
Patch density	0.162 \pm 0.144	1.27	0.040

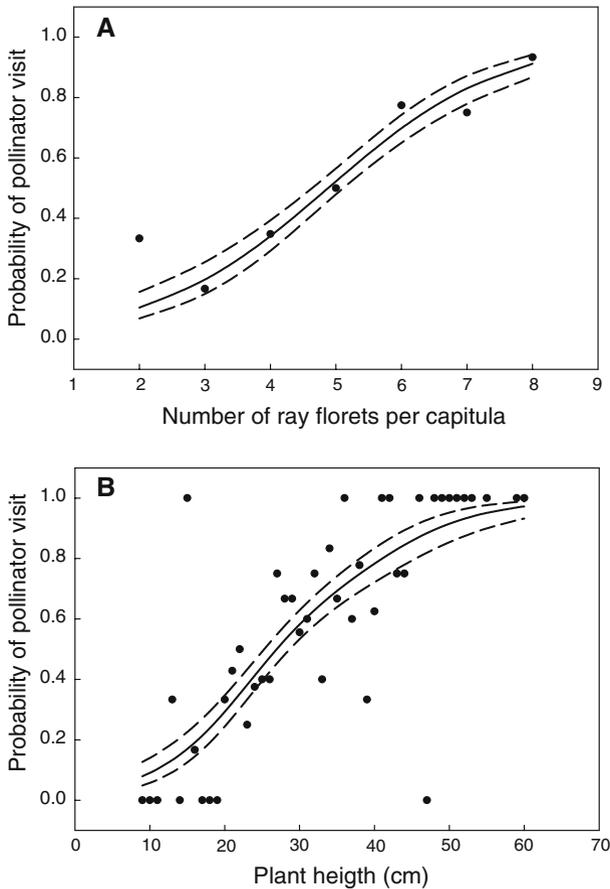


Fig. 2 Cubic spline estimates for the relationship between the probability of pollinator visit and (A) the number of ray florets (smoothing λ parameter = 2) and (B) plant height ($\lambda = 4$). The solid line is the estimated function fitted for the value of λ that minimizes the generalized cross-validation score (Schluter 1988). The dashed line represents ± 1 SE estimates from 1000 bootstrap replications. (See Table 2 for statistical analysis)

correlation, $r_{35} = 0.16$; $P = 0.35$; Fig. 3A), in the pollinator exclusion treatment the number of ray florets had a negative association with seed/floret ratio, suggesting a fitness cost associated with floral attractiveness ($r_{35} = -0.38$; $P = 0.021$; Fig. 3A).

Table 3 Analysis of covariance for seed/floret ratio. The number of ray florets was entered as covariate and the pollinator treatment (inclusion or exclusion) was a fixed factor

Factor	Df	F	P
Number of ray florets	1	1.919	0.170
Pollinator treatment	1	3.835	0.054
Number of ray florets \times pollinator treatment	1	6.41	0.015
Error	71		

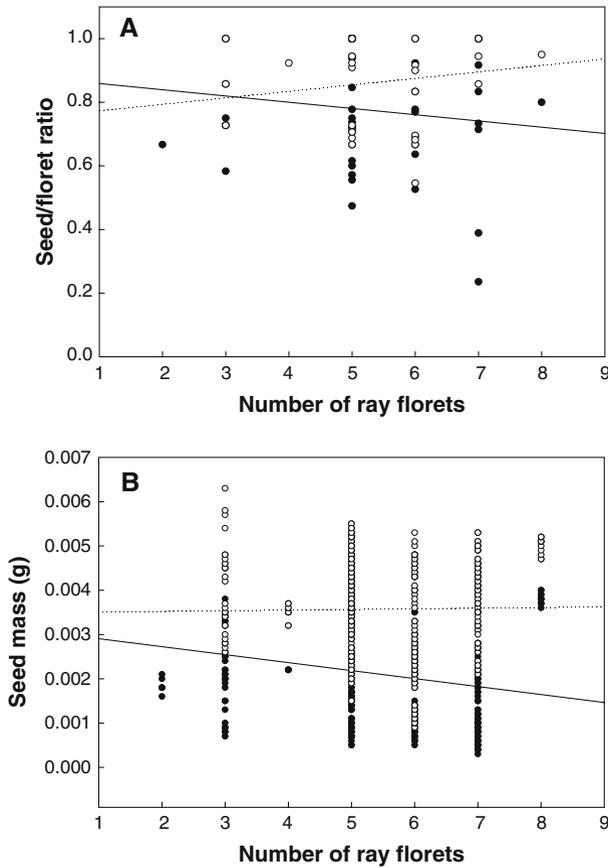


Fig. 3 Relationship between (A) the number of ray florets and the seed/floret ratio, and (B) the number of ray florets and seed mass, in pollinator-excluded (black circles, and solid line) and exposed capitula (open circles, and dotted line). (See Tables 3 and 4 for statistical analysis)

Seed mass

Variation in seed mass was significantly explained by the pollinator treatment and the interaction between number of ray florets and pollinator treatment (Table 4). Individual seed mass was significantly lower in capitula where pollinators were excluded (2.1 ± 0.064 mg) than in capitula open to natural pollination (3.5 ± 0.039 mg, Mean \pm SE; $P < 0.01$; t -test). While in the pollinator exposed treatment the number of ray florets was not correlated to seed mass ($r_{364} = 0.016$; $P = 0.73$; Fig. 3B), in the pollinator exclusion treatment the number of ray florets had a negative association with seed mass, suggesting another fitness cost associated with floral attractiveness ($r_{364} = -0.183$; $P < 0.0001$; Fig. 3B).

Seed germination

Seeds from capitula where pollinators were excluded showed lower germination ($50\% \pm 0.072$, Mean \pm SE) than that of seeds from control plants ($90\% \pm 0.029$)

Table 4 Analysis of covariance for seed mass. The number of ray florets was entered as covariate, type of floret (ray or disc florets) and pollination treatment were fixed factors

	Df	F	P
Number of ray florets	1	0.21	0.650
Pollinator treatment	1	7.72	0.005
Floret type	1	2.75	0.097
Number of ray florets × pollinator treatment	1	12.26	0.0001
Number of ray florets × floret type	1	1.03	0.311
Pollinator treatment × floret type	1	0.30	0.581
Number of ray florets × pollinator treatment × floret type	2	0.60	0.548
Error	769		

(Wilcoxon matched pairs test; $Z_{34} = 4.292$; $P < 0.0001$). Interestingly, germination percentage and number of ray florets had a (negative) correlation in the pollinator exclusion treatment (Spearman Rank Order Correlations; $r_{34} = -0.389$; $P = 0.021$) but not in the pollinator exposed treatment ($r_{34} = -0.248$; $P = 0.149$). Germination percentage was positively correlated to seed mass in the pollinator exclusion treatment ($r_{34} = 0.739$; $P < 0.0001$) but not in the treatment exposed to natural pollination ($r_{34} = -0.097$; $P = 0.578$).

Discussion

Our results suggest that the maintenance of within-population variation in the number of ray florets in *M. sativa* is explained, at least in part, by the balance between costs and benefits associated with this floral trait. Insect pollinators were strongly attracted by capitula with more ray florets, but in the absence of pollinators plants with more ray florets had lower fitness. As shown here, earlier work reported that dense patches, taller plants, and conspicuous floral traits increased pollinator visit (Cruzan et al. 1988, Galen 1989, Eckhart 1991, Galloway et al. 2002). Observational and experimental studies in other Asteraceae species showed that ray capitula received more visits than rayless capitula (Lack 1982, Stuessy et al. 1986, Andersson 1991, 1996, Olsen 1997, Nielsen et al. 2002).

In the study population, plants with conspicuous ray capitula should be selected due to pollinator preference, unless there were some costs associated with the attractive floral phenotype (Galen 1999, Anderson 2000, Elle and Carney 2003). Although pollinator visits significantly increased the success in flower-to-fruit conversion (seed/floret ratio ca. 10% higher than in pollinator exclusion treatment), *M. sativa* showed a high level of autogamy (ca. 77% seed/floret ratio in capitula with pollinator exclusion). Autogamy may allow reproductive assurance to plants when outcross pollination is limited (Darwin 1876, Stebbins 1970). Interestingly, only under pollinator exclusion there was a negative correlation between the number of ray florets and seed/floret ratio, suggesting that reproductive assurance was favored in plants with low allocation to floral attractive traits. A higher reproductive assurance in small flowers than in large flowers has been reported for *Collinsia parviflora* (Elle and Carney 2003). Resource investment in assuring reproduction may limit resource availability for floral attractiveness. Thus, manipulative experiments in *Nigella degenni* and *N. sativa* demonstrated the occurrence of fitness costs associated with the production of attractive floral structures (Andersson 2000, 2005).

Furthermore, maintenance of conspicuous floral traits could involve additional costs because water loss through inflorescences may place extreme demands on plant water economy, particularly in arid environments (Galen et al. 1999). The study area has a Mediterranean-type climate characterized by cool wet winters and dry summers (Di Castri and Hajek 1976). Because *M. sativa* reproduction starts during summer, water availability could be a limiting factor (Mooney and Dunn 1970). Galen et al. (1999) have shown that increase in corolla size in *Pollemonium viscosum* incurs a greater physiological cost in a population where flowering plants are water-stressed.

Costs associated with conspicuous capitula were also detected on seed mass and seed germination. The production of large flowers requires a higher investment of essential resources compared to the energy budget required for smaller, less conspicuous flowers (Andersson 2000, 2005). Several authors have demonstrated that flowers and seeds compete for the same pool of resources (reviewed in Ashman and Schoen 1996). Again, costs may be balanced against benefits, because pollinator exclusion meant a decrease in both seed mass and seed germination, which suggests the occurrence of inbreeding depression. It has been discussed that inbreeding depression may counteract the fitness benefits of increased seed production via autonomous selfing (Lande and Schemske 1985, Charlesworth and Charlesworth 1987).

Phenotypic correlations between floral and vegetative traits could constrain the evolution of conspicuous floral traits (Andersson 1997). Selective agents acting on other plant traits could limit the evolution of the focal trait if it is correlated with those traits (indirect selection) (Lande and Arnold 1983). Results showed that the number of ray florets is positively correlated with plant height and floral display. Further field research requires exploring if potential selective agents apart from pollinators (e.g. herbivores or competitors) could indirectly contribute to the maintenance of floral polymorphism in *M. sativa* via selection on correlated traits. For instance, previous work has shown that seed-predators prefer conspicuous flowers (Fenner et al. 2002, Cariveau et al. 2004). In the study system, at least one species of Tephritidae (Diptera) predate on immature seeds of *M. sativa* (González, personal observation).

The present study illustrates one benefit of conspicuous ray capitula of *M. sativa*: a strong preference by insect pollinators. It also demonstrates the occurrence of costs: when pollinators were excluded conspicuous ray capitula had a reduced reproductive assurance via autogamous selfing, and there were trade-offs between the number of ray florets and both seed mass and seed germination. Future research should explore these costs for mating system evolution using manipulative approaches, also addressing how environmental variation in the pollinator and seed predator community affects the selective scenario for floral phenotype. The extent to which the phenotypic selection detected in this study results in changes in the distribution of progeny phenotypes is presently unknown. The evolutionary response to selection depends on the magnitude of genetic variation of floral traits, which may be estimated performing experimental crosses between phenotypes. We are currently exploring the genetic basis of the floral characters of *M. sativa* herein studied. Patterns revealed by phenotypic selection analysis together with information on the heritability of floral traits will improve our understanding of how natural selection shapes floral evolution in this population.

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