

Male Reproductive Effort and Breeding System in an Hermaphroditic Plant

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Summary. Male reproductive effort was estimated from flower, seed and fruit biomass data in populations of the self-compatible plant *Gilia achilleifolia* that differ in genetically estimated selfing rate. Male reproductive effort decreases with increased rate of selfing, a finding that is consistent with theoretical arguments pertaining to the allocation of resources to male and female reproductive functions in hermaphroditic organisms.

Introduction

The allocation of resources to male and female function in hermaphroditic organisms has received much attention from theoreticians and experimentalists (Maynard Smith 1971; Charnov et al. 1976; Charnov 1979; Smith and Evenson 1978; Lovett Doust and Harper 1980; Vernet and Harper 1980; Lemen 1980; Fischer 1981; Lloyd 1980a; and Charlesworth and Charlesworth 1981). The problem is of interest because of its relevance to models for the evolution of dimorphic sexual expression (Charnov et al. 1976; Charlesworth and Charlesworth 1978a), and to recent arguments pertaining to the cost of sex (Williams 1975; Maynard Smith 1978; Lloyd 1980b). With regard to the latter mentioned topic, it has been postulated that self-fertilizing hermaphrodites should allocate proportionally fewer resources to male function than cross-fertilizing hermaphrodites (Maynard Smith 1971; Williams 1975; Lloyd 1980a; Charlesworth and Charlesworth 1981). Some researchers have suggested that the resources saved by reducing the allocation to male function may be channeled into the production of additional offspring, thereby reducing one of the proposed costs of sexual reproduction (Darwin 1877; Maynard Smith 1971, 1978; Heath 1977; Charlesworth and Charlesworth 1978a, b). In the angiosperms, self-pollinating hermaphrodites have been shown to have lower pollen/ovule ratios (Cruden 1977), but Charlesworth and Charlesworth (1981) have pointed out that this trend alone does not provide an adequate test of the hypothetical relationship between breeding system and male reproductive effort, since pollen/ovule ratios do not take into account the resource cost of maternal care accrued during the period between fertilization of the egg and dispersal of the seed. Several investigations of resource allocation to male and female function have been carried out with hermaphroditic organisms (Lovett Doust and Harper 1980; Lemen 1980; Fischer 1980), however these studies either lack the necessary accompanying measurements of selfing rate required to examine closely the relationship between male reproductive effort and degree of self-fertilization, or they have been performed with

outcrossing species. This report describes the pattern of reproductive resource allocation in different populations of the California annual plant, *Gilia achilleifolia* (Polemoniaceae), a species exhibiting a large degree of variation in rate of selfing (s). In this paper, male reproductive effort (m) is calculated according to the formula $m = a/(a + g)$, where a equals the resources allocated to male function, and g equals the resources allocated to female function.

Materials and Methods

Rates of natural selfing (s) were estimated for 7 populations of *Gilia achilleifolia* by progeny testing the families of open-pollinated parents at segregating alcohol dehydrogenase and phosphoglucosomerase loci. The genetic data so obtained were analyzed using maximum likelihood estimators of population genetic parameters (Brown and Allard 1970; Brown et al. 1975). The electrophoretic procedures and statistical methods applied have been described elsewhere (Schoen 1982).

To estimate m , two collections of plants were made in 1981 in each of the populations for which s had been previously estimated during 1979 and 1980. In the first collection, flowers were dried and separated into androecium, gynoecium, calyx, corolla, and pedicel. These parts were weighed to the nearest μg using an electrobalance (Cahn, model M-10), and mean weights were calculated. A second collection of plants was made towards the end of the growing season when the plants were in full fruit. Percent fruit set was determined by counting the persistent calyces (indicating the number of flowers per plant), mature fruits, and remnants of mature fruits. Mean fruit weights for each population were reconstructed from the seed set per fruit \times mean seed weight for the population, with the mean weight of the enlarged ovary minus the seeds added to this product.

In addition to these weight measurements, an experiment was undertaken to determine whether fruit and seed set are limited by low pollinator activity in populations with low selfing rates. All flowers in a group of treatment plants were cross-pollinated by hand with pollen from 2 plants located within a 2 m radius of each treated plant. Fruit and seed set were compared with a group of labelled control plants.

Results and Discussion

s ranges from 0.04–0.85 among the 7 populations (Table 1). s in this species is highly correlated with the degree of temporal separation between maturation of the anthers and the start of receptivity of the stigma within a flower (Schoen 1982). This latter characteristic is under genetic control, and there exists significant inter- and intrapopulation variation for it, suggesting

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Table 1. Data used in estimating male reproductive effort (\hat{m}) and its relation to estimated selfing rate (\hat{s}) in *Gilia achilleifolia*

Population ^a	$\hat{s} \pm \text{SE}^b$	Mean androecium weight (mg) $\pm \text{SE}$	Mean fruit weight (mg) $\pm \text{SE}^c$	Mean calyx + corolla + pedicel weight (mg) $\pm \text{SE}$	Mean proportion of flowers setting fruit $\pm \text{SE}$
San Ardo	0.20 \pm 0.05	0.628 \pm 0.044	10.528 \pm 1.567	1.561 \pm 0.104	0.790 \pm 0.027
Arroyo Seco	0.25 \pm 0.13	0.680 \pm 0.055	14.010 \pm 1.638	2.197 \pm 0.163	0.631 \pm 0.039
Poly Canyon	0.36 \pm 0.05	0.704 \pm 0.084	13.373 \pm 1.240	2.138 \pm 0.164	0.811 \pm 0.036
Metcalf Road	0.58 \pm 0.12	0.555 \pm 0.038	14.396 \pm 1.348	2.014 \pm 0.111	0.829 \pm 0.027
Arroyo Mocho	0.71 \pm 0.07	0.419 \pm 0.030	12.542 \pm 1.427	2.079 \pm 0.143	0.849 \pm 0.035
Eagle Ridge	0.85 \pm 0.07	0.408 \pm 0.023	15.600 \pm 1.810	2.032 \pm 0.150	0.977 \pm 0.012
F_s (d.f.)	populations ^d	6.679 ⁺ (5,54)	12.414 ⁺ (5,241)	2.643* (5,54)	9.966 ⁺ (5,74)
F_s (d.f.)	selfing rate ^d	27.717 ⁺ (1,59)	11.003 ⁺ (1,246)	0.455 (5,59)	24.281 ⁺ (1,79)
F_s (d.f.)	regression ^d	1.448 (4,54)	10.329 ⁺ (4,241)	2.992* (4,54)	3.669** (4,74)

* $P < 0.05$. ** $P < 0.01$. + $P < 0.001$.

^a Locations of populations given in Schoen (1982)

^b Selfing rate estimates based on 270–300 offspring genotypes from 30 parents in each population. Marker loci were obtained from alcohol dehydrogenase and phosphoglucose isomerase phenotypes (see Schoen 1982)

^c Larger fruits in the populations with higher \hat{s} are due primarily to higher seed set per fruit [Mean seed set per fruit in the 3 populations with the highest \hat{s} ($\bar{x} = 12.00$) was significantly greater than that for the 3 populations with lowest \hat{s} ($\bar{x} = 10.53$) ($F_s = 10.017$, d.f. = 1,246⁺). Mean seed weight did not differ significantly between these groups ($F_s = 1.375$, d.f. = 1,59)]

^d F statistics for analysis of variance among populations, between the groups of populations with the 3 highest versus the 3 lowest \hat{s} , and for deviation of data from linear regression on \hat{s}

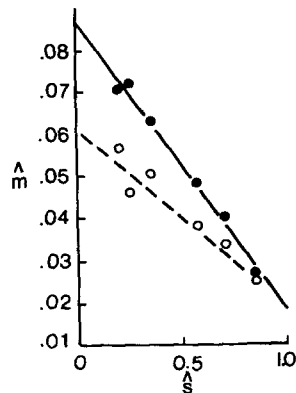


Fig. 1. Estimates of male reproductive effort (\hat{m}) in populations of *Gilia achilleifolia* with different estimated rates of self-pollination (\hat{s}). Closed circles for \hat{m} 's based on observed levels of fruit set. Open circles for \hat{m} 's based on hypothetical full fruit set. The correlation coefficients for the two sets of data are -0.99 ($P < 0.01$) and -0.96 ($P < 0.01$), respectively

that variation in \hat{s} among populations of *Gilia achilleifolia* reflects significant breeding system evolution rather than simple random fluctuations of this parameter (Schoen 1982). Table 1 lists the data relevant to the estimation of m . The amount of biomass allocated to reproduction per plant ($a + g$) was estimated in several ways. In the first set of calculations, a was assumed to equal the number of flowers per plant \times mean androecium weight for the population. g was assumed to equal the observed number of fruits per plant \times mean fruit weight for the population. The estimates of m (\hat{m}) based on a and g calculated in the above manner are highly negatively correlated with \hat{s} (Fig. 1). Since fruit set, but not seed set, appears to be limited by low pollinator activity in some populations of *G. achilleifolia* (Table 2), a second series of calculations were carried out in which g was assumed

to equal the maximum number of fruits that could be set per plant (i.e. all flowers developing into fruits) \times mean fruit weight for the population. Again, \hat{m} is highly negatively correlated with \hat{s} (Fig. 1). In each of these cases \hat{m} for the most extreme outcrossers is roughly twice that for the most extreme selfers.

The above calculations do not take into account the weights of corolla, calyx, and pedicel. When these additional weights are included in the estimation of m , a decision must be made as to how much of this biomass should be assigned to male function. Since there exist no objective criteria on which to base such a decision, \hat{m} was calculated for 3 hypothetical conditions, where the combined calyx, corolla, and pedicel weight was assigned: (1) completely to male function; (2) completely to female function; and (3) 50:50 to male and female function. In each of these cases, significant negative correlations between \hat{m} and \hat{s} were found (Table 3).

Assuming that amount of biomass accurately reflects the resource that limits overall reproductive effort, the findings reported here support the theoretical notion of reduced male reproductive effort in self-fertilizing hermaphrodites. Similar support comes from the studies of Lloyd (1972) on *Cotula* spp and Lemen (1980) on *Amaranthus* spp where pollen grain number per floret and anther volumes were found to decrease in species having increased likelihoods of selfing. Reduction of \hat{m} with increased \hat{s} in *Gilia achilleifolia* is due to both a decrease in androecium weight and an increase in fruit weight in the selfers (the latter trend is not linear) (Table 1). While it is not possible to determine whether the resources saved by reducing m are, in fact, redirected into the production and care of offspring, such a pattern is suggested by the fruit and seed set data. Selfers produce larger fruits than outcrossers (Table 1), and this trend does not appear to be the result of more assured pollination in the selfers, since seed set did not increase significantly in the normally outcrossing plants that received augmented pollination (Table 2). Furthermore, the potential for producing larger fruits is present at the

Table 2. Fruit and seed set in outcrossing populations of *Gilia achilleifolia* receiving augmented levels of cross-pollination^a

Population	δ	Mean proportional fruit set		t_s	Mean seed set per fruit		t_s
		with augmented pollination	without augmented pollination		with augmented pollination	without augmented pollination	
Arroyo Seco	0.25	0.773 ± 0.053	0.631 ± 0.039	2.183 (18)*	7.00 ± 0.45	6.00 ± 0.40	1.665 (72)
Hastings	0.04	0.836 ± 0.026	0.810 ± 0.036	0.921 (22)	10.11 ± 0.78	12.38 ± 0.83	1.391 (30)

* $P < 0.05$.^a See text for description of pollination treatment**Table 3.** Range of \hat{m} values and their correlation with δ when calyx, corolla, and pedicel weights are assigned varying degrees of male function

a based on total androecial weight + x% of the total combined weight of calyces + corollas + pedicels ^a			
g based on	x=0	x=50	x=100
observed fruit set	\hat{m} : 0.023–0.060 $r = -0.99^*$	\hat{m} : 0.081–0.150 $r = -0.92^*$	\hat{m} : 0.139–0.243 $r = -0.85^*$
full fruit set	\hat{m} : 0.023–0.049 $r = -0.99^{**}$	\hat{m} : 0.079–0.111 $r = -0.89^*$	\hat{m} : 0.135–0.175 $r = -0.75^*$

* $P < 0.05$, ** $P < 0.01$.^a Weight of calyces + corollas + pedicels that remains after assigning x% to male function is assigned to female function

floral stage in selfers; the number of ovules per ovary in the 3 populations with the highest δ 's ($\bar{x} = 15.66$) is significantly greater than that in the 3 populations with the lowest δ 's ($\bar{x} = 12.87$) ($F_s = 34.012$, d.f. = 1, 149, $P < 0.001$). Also relevant to the redirection of male resources is the higher fruit set in the selfers (Table 1). While increased fruit set in selfers is probably due, in part, to more assured levels of pollination, fruit set in plants from outcrossing populations that received augmented levels of cross-pollination is below that of the most extreme selfing population (Tables 1 and 2), suggesting that resources saved by reducing m may be channeled into the production of additional fruit.

The above findings are of particular importance with regard to models for the evolution of self-pollination (e.g. Solbrig 1976). In selfers, the genetic value of pollen is reduced, because of the decreased likelihood of outbreeding events (Charlesworth and Charlesworth 1981). Additionally, progeny produced via self-fertilization may be of lower fitness than those produced via outbreeding (due to inbreeding depression). Thus, a selfing parent may be able to increase the proportional representation of its genes in the next generation by producing more seeds, (compensating for the reduced survival probability of these inbred seeds) but not by producing more pollen or by maintaining pollen production at the present level. Redirection of the saved male resources may play an important role here. Alternatively, a redirection of male resources into growth and maintenance functions could increase parental fitness by reducing the risk of mortality associated with directing resources away from maintenance to reproduction (Gadgil and Bossert 1970).

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