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BROOD SIZE REDUCTION IN *LAVANDULA LATIFOLIA* (LABIATAE): A TEST OF ALTERNATIVE HYPOTHESES

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Abstract

Lavandula latifolia **(Labiatae) flowers have four ovules, yet fruits rarely bear more than two seeds due to extensive brood reduction. Tests of brood reduction hypotheses ascribing causal roles to genetic load, pollination shortage and resource (water and resources specific for seed maturation) limitation, were performed. In this species, brood reduction cannot be explained in terms of either pollen or resource limitation, and observed brood size patterns are not consistent with predictions from the genetic load hypothesis. A combination of ovary-level processes (sibling competition) and maternally predetermined patterns of ovule abortion most likely determine brood size in *L. latifolia*.**

Introduction

Low realized female fertility is widespread among flowering plants. The number of seeds produced usually represents a small fraction of the initial number of ovules, and this reduction in fecundity is the consequence of the juxtaposition of two distinct processes: fruit abortion (only a fraction of flowers mature fruits; fruit/flower ratio) and brood reduction (among successful fruits, only a fraction of the initial ovule complement develop into seeds; seed/ovule ratio) (Charlesworth, 1989). Adjustments of the fruit/flower and seed/ovule ratios may proceed independently of each other. In some species, experimental manipulations may modify the extent of either fruit abortion or brood reduction while being ineffective at modifying the other (Lee and Bazzaz, 1986; Stanton *et al.*, 1987; Gorchov, 1988; Andersson, 1990; Herrera, 1991). The two processes are often decoupled, and thus presumably represent independent responses to different selective pressures.

Whereas fruit abortion has received considerable theoretical and empirical attention in recent years, comparatively few studies have explicitly examined patterns of brood reduction (but see, e.g. Casper and Wiens, 1981; Bawa and Webb, 1984; Casper, 1984; Gorchov and Estabrook, 1987; Gorchov, 1988; Andersson, 1990), even though specific hypotheses and predictions have been available for testing for some years (Wiens *et al.*, 1987; Lee, 1988; Uma Shaanker *et al.*, 1988; and references therein). The present study examines brood size (number of seeds per fruit) patterns in *Lavandula latifolia* (Labiatae). Flowers of this species always have four ovules, yet fruits rarely have more than two seeds (Herrera, 1991). *L. latifolia* is an evergreen shrub common in the undergrowth of mixed woodlands at middle elevations in the eastern and south-eastern Iberian Peninsula. Most aspects of its reproductive biology have already been described (Herrera 1987a,b, 1988, 1989, 1990, 1991) and these details will not be repeated here. This paper presents a test of brood reduction hypotheses ascribing causal roles to genetic load, pollination shortage and resource limitation (see reviews in Lee, 1988; Uma Shaanker *et al.*, 1988; Charlesworth, 1989). Results are also discussed in relation to the parent-offspring conflict/sibling rivalry hypothesis proposed by Uma Shaanker *et al.* (1988).

Methods

This study was conducted during July–November of 1984 and 1986 on a population of *L. latifolia* growing at 1160 m elevation in the Sierra de Cazorla, Jaén province, south-eastern Spain [the 'Aguaderillos-1' site of Herrera (1988), where further details may be found].

The effect of additional pollination on brood size was investigated in 1984 on 10 *L. latifolia* plants. On each shrub, 10 experimental and 10 control (naturally pollinated) inflorescences were marked at the start of the flowering season. Every 7–10 days from mid-July to mid-October, all open flowers on experimental inflorescences were hand-pollinated using cross pollen. Treated flowers on experimental inflorescences, and open and newly withered flowers on control ones, were colour-marked on the calyx, using different colour codes on different dates. Four weeks after each flower marking and pollination session, the surviving colour-coded fruits were dissected individually without removing them from the plants. A longitudinal incision was made along the calyx using fine forceps, and the number of enclosed, nearly-ripe seeds was counted. This procedure was used because removal of fruits for examination, by altering the fruit set of flowers opening later on the same inflorescences (Tamas *et al.*, 1979), could interfere with other concurrent investigations on the same plants (Herrera, 1991). Brood size data for the entire reproductive season were combined for the analyses.

Water availability limits some components of fecundity in *L. latifolia* (Herrera, 1991), and it might also influence brood size. In 1984, brood size was determined for a total of 5524 fruits produced over the entire reproductive period by 13 plants under natural conditions. In 1986, seven of these plants were assigned to a watering treatment, and the remaining six individuals used as controls. Once a week, 25 l of water were poured around the base of each treated shrub. The first watering was done on 7 July, and the last on 5 September. A total of 1335 control and 2313 experimental fruits were examined over the entire reproductive season.

The effect of water availability on brood size was also investigated in combination with the effect of resources specific for seed maturation. In 1986, 1 × 1 × 1 m insect exclosures (made of wooden frames and 0.75 mm mesh size plastic netting) were placed on each of five large plants in early July, just before they started flowering, and held in place throughout their flowering periods. Exclosures precluded access of all floral visitors. Plants under exclosures flowered normally, but fruit production was negligible due to the lack of pollination (only 3.7% of flowers spontaneously set fruit, $N = 460$; as compared to 65.0%, $N = 16\,618$, in open pollinated flowers; Herrera, 1987a, and unpublished). Exclosure-covered plants were thus artificially relieved of the bulk of resource investment that would have represented the maturation of fruits produced under normal pollination conditions, and the consequences of the treatment were thus analogous to an increase in the amount of specific resources required for fruit maturation. Three of these experimental plants were also provided with additional water throughout the flowering period, using the same method and frequency of watering described above.

In each exclosure-covered plant, a small proportion of flowers relative to its total production (around 1%) was hand-pollinated with cross pollen at the middle of the flowering period (17–19 August), at a time when pollinator exclusion would have already 'saved' considerable resources to the plant, and the watering treatment (in the case of watered plants) had been underway for time enough (1.5 months) to be potentially effective. Fruits produced were collected 4 weeks later, and seeds were counted and individually weighed. Brood size data from the seven watered, open pollinated, and the six not watered, open pollinated plants used in the watering experiments described above were used as controls, but only the subsample of fruits produced by flowers that were open between 9–19 August were considered.

The hypothesis that brood reduction was due to genetic load was examined indirectly. If mutational load is responsible for brood reduction, the abortion of individual seeds will be determined by the zygote genotypes; non-developing seeds will occur randomly within fruits, and the failure of an ovule should be independent of the failure of the other ovules in the same flowers (Gorchov and Estabrook, 1987; Charlesworth, 1989). In the case of *L. latifolia*, where the number of ovules per flower is fixed, brood size should be expected to conform to a binomial distribution with parameter p equal to the overall probability of occurrence of a genetically viable embryo. The prediction may thus be tested by comparing observed brood size frequencies with those expected from the binomial distribution. As different plants will differ in genetic constitution, the probability of a seed being inviable for genetic reasons would differ among individuals, and separate tests will be performed for the 15 study plants. For each plant, brood size data for 1984 and 1986 were combined into a single sample (no significant between-year variation was found; Herrera, 1991).

Brood size frequency distributions are truncated (no zero term), and an iteration method was used for binomial fitting. An array of expected binomial frequencies (p-values ranging between 0.01 and 0.99) was generated for each individual plant. The observed brood size distribution was compared to the truncated portion of each expected distribution, and a chi-square obtained in each comparison. For each plant, the smallest chi-square was retained and used as a measure of goodness of fit. Standard chi-square significance tables were not appropriate (assumptions of the chi-square test are not met by the procedure used here), and significance tables were generated by simulation. For each plant, 500 brood size frequency distributions were simulated, each consisting of 200 randomly extracted 'fruits' from a binomial distribution with p equal to the probability which minimized the chi-square between observed and expected brood size distributions. The cumulative frequency distributions of minimum chi-squares (obtained using the same iterative algorithm as above) were used as significance tables. Critical values for significance eventually proved to be independent of p ($H = 11.81$, df $= 10$, $P = 0.30$; Kruskal–Wallis analysis of variance), and a single significance table was obtained by pooling all simulated distributions.

Analyses of experimental data were performed with the GLM procedure in SAS, using Type III sum of squares due to the unbalanced nature of the data (SAS Institute, 1987). Original data on number of seeds per fruit were transformed for the analyses using the Freeman–Tukey square root transformation (Zar, 1984: 241). Throughout this paper, all means are reported ±1 SD.

Results

Brood size reduction in *L. latifolia* is not attributable to insufficient pollination, as fruit seediness was not increased by experimental pollen addition. Distributions of brood size were positively skewed in both experimentally pollinated and control fruits (Fig. 1). The shapes of the two distributions were statistically indistinguishable ($P = 0.32$, Kolmogorov–Smirnov two-sample test), and experimental and control fruits did not differ in mean brood size ($F = 0.22$, df = 1,5243, $P = 0.64$). For the two groups of fruits combined ($N = 5244$), most fruits had either one (54.4%) or two (39.3%) seeds. Only 6.3% of fruits had three/four seeds.

Observed distributions of brood size for individual plants are not consistent with the genetic load hypothesis for brood reduction. In 13 out of 15 plants, the observed frequencies of differently-seeded fruits departed significantly from those expected from a binomial distribution (Table 1). There was a consistent pattern in the departure of individual brood size classes from binomial expectations. Fruits with two seeds were generally overrepresented, and those with one, three and four seeds underrepresented, with respect to binomial expectations.

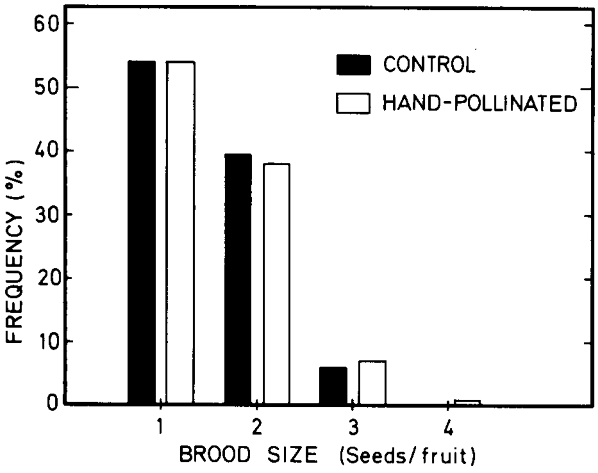

Fig. 1. Frequency distributions of brood size in *Lavandula latifolia* fruits from control (naturally pollinated; $N = 4014$ fruits) and hand-pollinated ($N = 1230$ fruits) flowers.

The effect of supplemental water on brood size (accumulated over the entire reproductive season) was tested using a two-way ANOVA with interaction. The 1986 watering treatment was used to define two groups of plants: 'Group 1', plants not watered in any year; and 'Group 2', those watered in 1986 but not in 1984. Two levels existed within each group, corresponding to the

Table 1. Frequency distributions of numbers of seeds per fruit on an individual plant basis (N = number of fruits examined). Fit of observed distributions to a truncated binomial was tested using an iterative algorithm (see text), and significance of departure is shown here (*, $P < 0.05$; ***, $P < 0.0001$). For distributions departing significantly from the binomial, the relative departures of brood size classes with respect to expected binomial frequencies are also shown (+, observed > expected; –, observed < expected)

Plant	*N*	Proportion of fruits (%)				Departure from binomial		Departure from expected			
		Number of seeds						Number of seeds			
		1	2	3	4	Chi-square	Significance	1	2	3	4
A1	676	78.3	21.0	0.7	0	7.6	*	–	+	–	–
A2	501	64.3	35.7	0	0	38.9	***	–	+	–	–
A3	391	40.5	48.3	10.7	0.5	20.4	***	–	+	–	–
A4	120	58.4	33.3	8.3	0	0.9	$P > 0.40$				
A5	337	76.3	23.4	0.3	0	8.1	*	–	+	–	–
B1	696	60.3	37.8	1.9	0	40.3	***	–	+	–	–
B2	1069	78.8	21.0	0.2	0	21.3	***	+	+	–	–
B3	801	57.6	39.4	3.0	0	42.4	***	–	+	–	–
B4	802	67.8	31.8	0.4	0	41.8	***	–	+	–	–
B5	307	85.7	14.0	0.3	0	1.4	$P > 0.55$				
C1	1125	54.9	41.5	3.6	0	65.5	***	–	+	–	–
C2	1035	30.6	44.4	23.0	2.0	21.5	***	–	+	+	–
C3	1259	52.3	44.8	2.9	0	111.4	***	–	+	–	–
C4	1273	53.1	43.3	3.5	0.1	89.6	***	–	+	–	–
C5	408	34.3	51.5	14.2	0	31.9	***	–	+	–	–

two study years. Year and 'group' were used as main effects. Significance of the interaction term would reveal an influence of watering on brood size. The group effect was highly significant (Table 2), indicating that the two subsets of plants differed in mean fruit seediness. After accounting for this difference, neither the year effect nor the interaction term was significant. Mean brood size thus remained invariant between years, and it was unaffected by watering.

The combined effects of resources and water on brood size were examined by means of a two-way ANOVA with interaction (Table 3). There was no significant effect of additional water, and a highly significant effect of additional resources, on brood size. The water × resources interaction term was also significant. Considering separately the subset of plants that were not watered, there was no significant difference in mean brood size (in parentheses) between control plants (1.47 ± 0.64, $N = 350$) and those with additional resources (1.48 ± 0.56, $N = 71$) ($F = 0.03$, df = 1,419, $P = 0.86$; one-way ANOVA). In contrast, when watered plants are considered separately, brood size of control plants (1.26 ± 0.45, $N = 518$) was significantly lower than that of plants with additional resources (1.72 ± 0.68, $N = 167$) ($F = 97.5$, df = 1,683, $P \ll 0.0001$). Additional water alone was thus ineffective at increasing brood size, and additional resources were effective only in combination with increased water availability. Nevertheless, and despite its statistical significance, the combination of water and resources resulted only in a weak increase in brood size, and considerable brood reduction still took place in these experimental plants. Among these, the proportions of fruits with one, two and three/four seeds were, respectively, 40.5%, 47.0% and 12.5%, as compared with 59.7%, 33.7% and 6.6% among control plants (neither additional water nor resources).

The influence of brood size and watering treatment on seed size was examined using seed mass data from the fruits produced by hand-pollinated flowers in the five exclosure-covered plants (Table 4). There was a highly significant effect of brood size on seed mass. Mean

Table 2. ANOVA table for the effects of year and 'group' of plants on the number of seeds per fruit in *Lavandula latifolia* (1984 and 1986). Plants were assigned to either of two groups, depending on whether or not they received artificial watering in 1986. Data were square root-transformed for the analysis

Source	df	Type III sum of squares	Mean square	F	P
Year	1	0.07929	0.07929	0.47	0.49
Group	1	38.01695	38.01695	226.04	$\ll 0.0001$
Year × Group	1	0.13395	0.13395	0.80	0.37
Residual	9168	1541.95989	0.16819		

Table 3. ANOVA table for the effects of water and resources on the number of seeds per fruit in *Lavandula latifolia* Seed number data were square root-transformed for the analysis

Source	df	Type III sum of squares	Mean square	F	P
Water	1	0.00756	0.00756	0.05	0.82
Resources	1	4.35339	4.35339	28.61	$\ll 0.0001$
Water × resources	1	3.83256	3.83256	25.18	$\ll 0.0001$
Residual	1102	167.70357	0.15218		

Table 4. ANOVA table for the effect of additional water (treatment) on seed weight of exclosure-covered (provided with additional resources) *Lavandula latifolia* plants. The number of seeds per fruit (brood size) was included in the analysis as a covariate, and plants were nested within treatments

Source	df	Type III sum of squares	Mean square	F	P
Treatment	1	0.53728	0.53728	4.88	0.028
Brood size	2	3.41842	1.70921	15.51	0.0001
Treatment × brood size	2	0.21478	0.10739	0.97	0.38
Plant (treatment)	3	5.25579	1.75193	15.90	0.0001
Brood size × plant (treatment)	5	1.07925	0.21585	1.96	0.084
Residual	378	41.65292	0.11019		

seed mass decreased steadily as brood size increased (1.58 ± 0.43 mg, $N = 107$; 1.37 ± 0.34 mg, $N = 218$; 1.28 ± 0.33 mg, $N = 67$; for fruits with one, two and three/four seeds, respectively). After accounting for this effect and for the significant difference between individual plants in seed mass, the effect of the watering treatment on seed weight was also significant. Seeds from watered plants were heavier (1.44 ± 0.39 mg, $N = 287$) than those from plants that were not watered (1.34 ± 0.32 mg, $N = 105$). The brood size × treatment interaction was not significant, and the proportional increase in seed mass brought about by watering was roughly similar across brood-size classes (Fig. 2).

Discussion

The brood reduction consistently exhibited by *L. latifolia* cannot be explained in terms of either pollen or resource limitation. Experimentally providing the plants with extra pollen, water and specific resources for seed maturation, did not increase the number of ovules that developed into seeds within individual fruits. Although the combination of additional water and resources resulted in a statistically significant increase in brood size, the change was quantitatively negligible, and extensive brood reduction still took place in these experimental plants. These results confirm previous investigations, most of which have found that brood size is independent of resource and pollen availability (e.g. Marshall *et al.*, 1986; Snow, 1986; Stanton *et al.*, 1987; Wiens *et al.*, 1987; Gorchov, 1988; Uma Shaanker *et al.*, 1988, and references therein; but see, e.g. Delph, 1986; Zimmerman and Pyke, 1988, for exceptions).

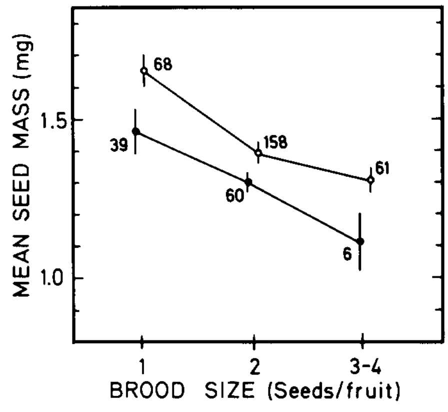

Fig. 2. Variation in mean mass of individual seeds according to brood size and watering treatment (open dots, watered plants; filled dots, control plants). Vertical lines extend over ±1 standard error of the mean. Numbers are sample sizes (number of seeds) in each category. See Table 4 for statistical analysis.

Although interspecific patterns of brood size tend to be consistent with the genetical load hypothesis of brood reduction (Wiens, 1984), studies of individual species have provided contrasting results (Bawa and Webb, 1984; Gut and Weller, 1986; Mazer *et al.*, 1986; Gorchov and Estabrook, 1987; Wiens *et al.*, 1987; Andersson, 1990). The data for *L. latifolia* are not consistent with this hypothesis. In almost all individuals, brood size distributions departed significantly from binomial expectations. Within fruits of the same plant, therefore, the failure of individual seeds was not independent of the fate of other seeds in the same fruit, suggesting that ovule failure was not due to developmental problems arising from the random occurrence among embryos of developmental lethals (Gorchov and Estabrook, 1987; Charlesworth, 1989).

In addition to the set of 'classical' hypotheses tested in this paper with negative results, one further hypothesis, proposed by Uma Shaanker *et al.* (1988), could help to explain brood reduction in *L. latifolia*. According to it, brood reduction is the consequence of a combination of parent–offspring conflict and sibling rivalry ('PC–SR hypothesis' hereafter). Although brood size data for *L. latifolia* were not gathered specifically for testing the PC–SR hypothesis, some of the results presented here are appropriate for evaluating it.

A prediction of the PC–SR hypothesis states that positively skewed distributions of brood size should be associated with species in which the fruit or a discrete part thereof is the unit of dispersal, while negatively skewed distributions will be associated with species in which seeds rather than fruits are the units of dispersal (Uma Shaanker *et al.*, 1988). Data for *L. latifolia* do not support this prediction. In this species, the seed is the unit of dispersal (after maturation, nutlets become loose within the calyx and are dispersed independently), yet the frequency distribution of brood size is positively skewed. This suggests that, if parent–offspring conflict actually exists in *L. latifolia*, it is predictably decided in favour of the offspring's interests (seeds from small broods are heavier than those from large ones, and are thus expected to have a greater post-germination success).

L. latifolia plants actually have the ability of increasing reproductive output in response to extra resources. When provided with additional water, flower production and fruit set experience significant increases (Herrera, 1991). Nevertheless, the same plants are apparently unable to take further advantage of additional water by increasing brood size, which suggests little maternal capacity for short-term regulation of this component of reproductive yield. The inability of *L. latifolia* plants to modify brood size in response to increased resources might be explained in terms of the PC–SR hypothesis, as it predicts that brood reduction in species with few ovules per flower will more often be due to sibling rivalry than to maternal regulation (Uma Shaanker *et al.*, 1988). On the other hand, the lack of brood size regulatory ability by the mother plant may be just the consequence of this magnitude being genetically or developmentally predetermined (Casper and Wiens, 1981; Guth and Weller, 1986; Mazer *et al.*, 1986; Andersson, 1990). Supporting the first interpretation is the observation that additional water, while being ineffective at increasing brood size, did result in increased seed size. If brood reduction is largely a consequence of within-ovary sibling competition, one would not expect increased resources to prevent it completely, but rather to find a greater final advantage (size) of the competitively dominant offspring, as found here. In favour of the second interpretation is the existence of significant individual differences in brood size and their consistency among years. Individual variation in mean brood size was more consistent among years than that of other reproductive parameters (inflorescence production, flower production per inflorescence, fruit set) (Herrera, 1991).

These two interpretations of brood size reduction in *L. latifolia* (within-ovary competition, and genetically or developmentally predetermined brood size) are not mutually exclusive, and a complex combination of ovary-level processes and maternally predetermined patterns of ovule abortion most likely accounts for observed brood size patterns in this and other species with a fixed, small number of ovules per flower (Casper and Wiens, 1981; Weller, 1985; Gorchov and Estabrook, 1987; Casper, 1984, 1988; Andersson, 1990). Differential relative importance of the two processes in different species, and the practical difficulty inherent in separating brood reduction mediated by selective embryo abortion ('infanticide') from that resulting from sibling competition ('fratricide'), could help to explain some of the contrasting results found in the literature (e.g. Casper, 1988; Andersson, 1990).

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