

Blooming times of individual inflorescences and plants as determinants of flower and fruit predation in *Lavandula stoechas* (Lamiaceae)

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Abstract

The intensity of flower and fruit destruction by insect predators, as well as percent fruit-set in inflorescences of *Lavandula stoechas* L., a common Mediterranean shrub, were investigated in relation to the blooming time of the inflorescence, the flowering peak of the individual plant relative to that of the population, and plant identity. The intensity of flower predation (by beetles of the genus *Meligethes*, Nitidulidae) correlated positively with blooming intensity at both plant and population levels, whereas a similar relationship was lacking for fruit predation rates by parasitic wasps of the genus *Eurytoma*. Within-plant phenological variations in inflorescence blooming time accounted for most of the variance in fruit-set, although a significant effect of inter-plant variations in phenology, along with a (weaker) effect of plant identity also existed. It is concluded that flower and fruit predation rates may represent only minor selective pressures on this plant's current phenology.

Keywords: Mediterranean, Lamiaceae, *Lavandula*, Phenology, Fruit-set, Predation.

Resume

On a étudié l'intensité de la destruction des fleurs et des fruits par les insectes prédateurs, ainsi que le pourcentage de formation de fruits dans des inflorescences de *Lavandula stoechas* L., un arbuste méditerranéen commun, en relation avec l'époque d'épanouissement des inflorescences, le pic de floraison des individus par rapport à celui de la population, et l'identité de la plante. L'intensité de prédation des fleurs (par des coléoptères du genre *Meligethes*, Nitidulidae) est corrélée positivement avec l'intensité de floraison, aussi bien au niveau de la plante qu'à celui de la population, tandis qu'une relation similaire n'existe pas pour les taux de prédation des fruits par les guêpes parasites du genre *Eurytoma*. Les variations phénologiques intra-plante de l'époque d'épanouissement de l'inflorescence rendent compte de la plus grande part de la variance dans la formation des fruits, même s'il existe un effet significatif des variations inter-plantes dans la phénologie, ainsi qu'un effet (plus faible) de l'identité de la plante. On en conclut que les taux de prédation des fleurs et des fruits peuvent ne représenter que des pressions sélectives mineures sur la phénologie actuelle de cette plante.

INTRODUCTION

Increased visitation rate by flower-feeding animals to synchronously blooming individuals is accepted to have selected this kind of flowering behaviour in plants (SCHI:MSKE, 1977, 1978; WASER, 1979; AUGSPURGER, 1981; WYATT, 1982; STEPHENSON, 1982; GROSS & WERNER, 1983; JENNERSTEN *et al.*, 1988; see RATHCKE & LACEY, 1985, for a review). In addition, and by preferentially attacking reproductive structures at certain moments and densities, flower and fruit predators have also probably contributed to shape plant phenology (JANZEN & WILSON, 1977; ZIMMERMAN, 1980; AUGSPURGER, 1981; ZIMMERMAN & GROSS, 1984; MOLAU *et al.*, 1989; PETERSSON, 1991).

Logically, the existence of inter-individual variations in phenology is a precondition for predators to exert any pressure on this plant trait. And, however, there is also in any plant species an amount of variation occurring within individuals (i.e., not all the flowers in a plant are open at the same time) which may hinder the evolution of phenological shifts. This kind of variation is often ignored in pollination studies, fruiting being most often reported at the individual level with no control for within-plant variations (for example, ZIMMERMAN & GROSS, 1984; DIERINGER, 1991; ENGLISH-LOEB & KARBAN, 1992). Comparing the effects of both within- and among-plant variability on reproduction would help to get a more realistic picture of how plants, pollinators and predators interact.

In this study I report estimates of flower and fruit predation, as well as final fruit-set at the inflorescence and individual levels in *Lavandula stoechas* L. (Lamiaceae), a xerophytic shrub common in southern Spanish scrub. Flowers and developing fruits are attacked by several insect predators (*see below*), and because relatively few fruits abort and relatively few flowers remain unpollinated, fruit-set and predation intensity are strongly and negatively correlated. This makes *L. stoechas* a suitable organism to study how phenology and predation interact.

MATERIAL AND METHODS

L. stoechas is a xerophytic, sun-loving aromatic shrub up to 1 m high which in southern Spain grows and blooms during late winter and early spring (February through May; HERRERA, 1986). Flowers are hermaphroditic and tubular (*see* HERRERA, 1991), have a dark purple corolla, and secrete minute amounts of sugar-rich nectar (HERRERA, 1985). Flowers are heavily visited by bombylid flies and bees (HERRERA, 1988) which, coupled with self-compatibility (Munoz & DEVESA, 1987), regularly results in heavy fruiting. Pollen: ovule ratio is about 1 000, and spontaneous autogamy is below 1% (HERRERA, 1987). Fruits may contain 1-4 brown, 2 mm long nutlets (seeds, hereafter) which remain enclosed within the calyx until dispersal (June-July; HERRERA, 1986).

L. stoechas flowers are grouped into heads which appear at the top of a long peduncle. Heads are nearly cylindrical, 2-3 cm long aggregations of dichasia terminated by several (4-6) showy purple bracts (for a more complete description of inflorescence structure *see* HERRERA, 1991). Each head opens about 100 flowers spread over a period of 3-4 weeks, although relatively few flowers open during the first week. Maxima occur during the second week and later, the pattern of within-head flower abundance being thus typically left-skewed (DEVESA *et al.*, 1985). At the plant level, flowering commonly lasts 2-3 months (medium-sized plants produce about 30 inflorescences) and the shape of an individual's flowering curve is also left-skewed (HERRERA, 1986, and unpublished data). As a result, plants come into

bloom slowly while end abruptly. Individual flowering periods are highly overlapping in this species (overlap has been shown to rank second in a sample of 30 scrub species; HERRERA, 1986).

Field work was done at the Reserva Biológica de Doñana (Doñana National Park, southern Spain), a coastal area with a Mediterranean climate (see RIVAS-MARTINEZ *et al.*, 1980, for a description of vegetation in the area). The study site is that used by HERRERA (1991) and comprises a stand of xerophytic scrub with *L. stoechas* growing on old, stabilized sand dunes.

Phenology

To monitor flowering phenology, I tagged 19 randomly chosen *L. stoechas* plants before the onset of flowering. In this sample, among-plant distances ranged from five to 100 m, and eventual inflorescence production from four to 146 per individual (mean \pm s.e., $X = 31.6 \pm 8.8$; sum, 601 inflorescences; $N = 19$ plants). It was known from a previous study (HERRERA, 1986) that this population is highly synchronic at flowering, so the sample was expected to encompass most or all of the existing phenological variation. All through the flowering season (see fig. 1) I monitored individual flowering phenologies by noting, on a weekly basis, the number of flowering heads (i.e., with at least one flower open) on each plant. At each inspection, I also marked and numbered a sample of newly opened inflorescence buds. By the time the fruits were ripe (late June), tagged inflorescences were harvested and preserved in a freezer at -30°C . The date of first bloom for any of these inflorescences was known with an error of \pm one week.

Assessing predation rates and fruit set in all the 19 marked shrubs would have been impractical because the process of getting accurate estimates for these variables is extremely time-consuming. Thus, inflorescence inspection was restricted to a subsample of eight individuals encompassing the whole phenological variability of the large sample. Out of the 19 original plants, and starting on January 20th, four individuals attained peak bloom on day 51, nine on day 58, and six on day 80 (see fig. 1). I thus randomly selected a number of individuals within each of these three phenology-based groups of plants: respectively, two, four, and two plants with either early, middle, or late blooming peaks relative to the population's peak were chosen. The remaining 11 plants were thereafter ignored.

For each plant in the subsample, preserved inflorescences were ranked by flowering date. Then, five in which the blooming date preceded, and five in which the blooming date occurred after the individual's flowering peak were chosen. This allowed to control the effect of within-plant (among-inflorescence) phenological variations on predation and fruit-set, in addition to the effect of among-plant variations. Thus, 10 inflorescences per plant were studied, except for an individual in which only eight inflorescences were available. In all, 78 inflorescences were inspected.

Estimates of predation and fruit-set

The two main predators of *L. stoechas*'s reproductive structures are a beetle and a chalcidoid wasp (personal observation). Larvae and adults of *Meligethes* sp. (Coleoptera, Nitidulidae) mostly damage flowers by chewing anthers, styles and ovules. This type of predation can be easily recognized at fruiting by calyces containing only remains of floral parts together with droppings and cuticles shed by larvae. Damages caused by the other major predator, the larvae of *Eurytoma* sp. (Hymenoptera, Eurytomidae, Chalcidoidea), are more cryptic: a single larva eats the content of one seed, pupates, and finally emerges as an adult through a hole in the apparently viable seed. Prior to emergence, seeds often show no external sign of attack, so every seed has to be individually cut with a blade to detect unemerged larvae. As a result of the oviposition strategy by *Eurytoma* females, no seed escaped predation in wasp-attacked fruits: if a parasitized nutlet appeared within a calyx, the others most often had been preyed too. Consequently, fruit predation behaved like a two-state variable (preyed or not) and data below pay no attention to the number or proportion of seeds destroyed within fruits.

On average, 20-30 calyces were examined per inflorescence which represents about 30% of overall flower number. In all, 1 603 calyces were inspected. The rate of flower predation of any inflorescence is defined in the present study as the ratio of flowers destroyed by *Meligethes* to the total number of calyces inspected in this inflorescence. Fruit predation is the ratio of *Eurytoma*-attacked fruits to the

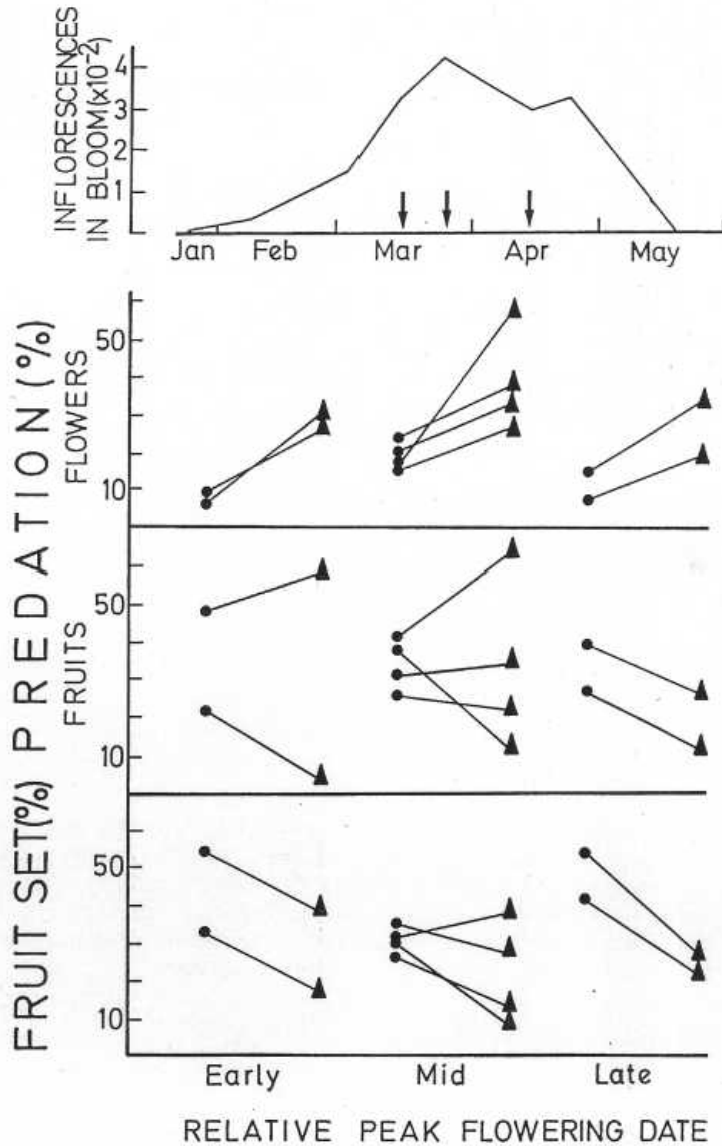


FIG. 1. - The relationship between flowering phenology and flower-fruit predation rates at Donana, southern Spain. Top: overall flowering phenology for 19 *L. stoechas* plants. The curve represents changes in the total number of inflorescences in bloom (in hundreds). Arrows point to peak flowering dates of individuals. Bottom: flower predation, fruit predation, and fruit set in eight *L. stoechas* plants with a flowering peak either previous, coincident, or subsequent to the population's blooming peak (arrows in top graph). Symbols represent averages for inflorescences coming into bloom during the first (circles) or second (triangles) half of an individual's flowering period. Lines connect averages for each plant.

total number of fruits (i.e., calyces containing at least one seed, damaged or not). Finally, fruit-set is the ratio of good fruit (i.e., calyces containing only undamaged seeds, with no sign of predation) to the total number of calyces observed. All three variables were determined for each of the 78 study inflorescences.

Data analyses

Flower and fruit predation and final fruit-set were the dependent variables in a MANOVA where inflorescences were cases and main factors were phenological variations and plant identity. Among-plant variations in phenology were accounted for in the MANOVA by factor PEAK, which had three levels (i.e., an individual's peak might occur before, at the same time, or after most plants in the population). Within-plant variations were accounted for by factor MOMENT, which had two levels (i.e., inflorescences may come into bloom during the first or the second half of that plant's flowering period). The third main factor (plant identity) was accounted for by PLANT, which was nested under PEAK. Finally, the interaction between PEAK and MOMENT was also included in the model. Univariate and multivariate statistics were then computed with the GLM procedure of the SAS package (SAS, 1987). Predation and fruiting rates were arcsine-square root transformed (SOKAL & ROHLF, 1981) and checked for normality prior to analyses.

RESULTS

The overall flowering phenology of the *L. stoechas* population during the year of study is shown in [figure 1](#). As a whole, flowering extended from February through mid-May, the highest number of inflorescences in bloom being observed by the end of March, at which moment a large proportion (c. 50%) of the plants had their blooming peaks (*see* Methods). About half of the individuals, however, reached peak bloom earlier or later in a period roughly encompassing one month (from mid-March through mid-April).

The proportion of flowers destroyed by predators within any inflorescence correlated well with phenology: those inflorescences coming into bloom during the second half of an individual's flowering period had more of their flowers damaged, and this holds for any of the eight study plants ([fig. 1](#)). As a result, a highly significant effect of within-plant phenological variability on flower predation was detected ([table I](#)). Moreover, a significant effect of among-plant variations also occurred through which phenologically modal plants lost more flowers to predators than non-modal ones.

In contrast to flowers, there was no indication that the proportion of fruits destroyed by predators was related to phenological variability at either plant or population levels. In some plants, earlier inflorescences suffered more damage, whereas in others the opposite occurred ([fig. 1](#)). Consequently, no statistically significant effect of either within- or among-plant phenological variations was apparent ([table I](#)). Plant identity was the only factor to explain a significant part of the variance in fruit predation.

Percent fruit set was sensitive to all three main factors considered. With a single exception, all plants had more fruit set in early- than in late-flowering inflorescences ([fig. 1](#)). Phenologically modal plants, on the other hand, had lower averages than non-modal ones. The effect of plant identity was also significant ([table I](#)).

Multivariate statistics in [table I](#) show that all three main factors were significant in the MANOVA, although their power to explain the observed variance were to a great extent different. Within-plant phenological variations explained most of the variation; plant identity accounted for much less; and the phenology of the individual plant was hardly significant.

TABLE I. – Results of MANOVA on the percentages of flowers and fruits preyed upon, and final fruit set in *L. stoechas* inflorescences. Predictor variables are the date of the individual's flowering peak relative to the population's peak (identified as *PEAK*), plant identity (nested within *PEAK*), and the moment on which any inflorescence came into bloom relative to the plant's general flowering period (i. e., within-plant variability, identified as *MOMENT*).

UNIVARIATE STATISTICS						
VARIABLE	R2	Source	DF	MS	F	Pr> F
FLOWER PREDATION	0.466	PEAK	2	755	6.09	.003
		PLANT (PEAK)	5	153	1.24	ns
		MOMENT	1	4 416	35.58	1.E-07
		PEAK*MOMENT	2	64	0.52	ns
		Error	67	124		
FRUIT PREDATION	0.289	PEAK	2	324	0.82	ns
		PLANT (PEAK)	5	1 888	4.76	< .001
		MOMENT	1	453	1.14	ns
		PEAK*MOMENT	2	187	0.47	ns
		Error	67	396		
FRUIT SET	0.434	PEAK	2	511	5.18	.008
		PLANT (PEAK)	5	437	4.43	.001
		MOMENT	1	1 797	18.20	6.E-05
		PEAK*MOMENT	2	41	0.42	ns
		Error	67	98		
MULTIVARIATE STATISTICS						
Source	Wilks' Lambda	DF	F	Pr > F		
PEAK	0.785	6/130	2.78	.013		
PLANT (PEAK)	0.607	15/180	2.37	.003		
MOMENT	0.541	3/65	18.35	1.E-08		
PEAK*MOMENT	0.900	6/130	1.16	.327		

DISCUSSION

As stated above (*see* Material and Methods) individuals of *L. stoechas* bloom very synchronously, and also the inflorescences within individual plants overlap their flowerings to a great extent. In spite of this, there are distinct "peaks", that is, moments at which flowers are more numerous at the inflorescence, plant, and population levels and, according to the present study, predators do track such changes. It could be argued that the sample used in this study (eight individuals) was low, although it could also be defended that detecting a significant pattern with such a low number is, if something, indicative of a real trend. The key point, however, is that eight individuals were enough to depict the scarce phenological variation within the population.

The slight predation of flowers in those inflorescences that come into bloom during the first half of the plant's flowering period (i.e., the left, few-flowered tail of the curve) comparative to those flowering later (table I, fig. 1) is consistent with the notion that the attack of *Meligethes* beetles is highly density-dependent. Heavier flower destruction by beetles in phenologically modal plants when compared with non-modal ones (table I) is also indicative of a positive response to increased flower abundance.

In contrast with flowers, the predation of fruits by Chalcidoid wasps lacked any significant phenological pattern: the proportion of fruits lost to wasps could be low or high in any inflorescence regardless of the particular moment at which it came into bloom within the plant, just as plants could experience high or low predation averages regardless of their phenological position within the population (fig. 1). The density of *L. stoechas* flowers in January was as low as one would expect in a population that is just starting to bloom, yet one plant was found to lose an average of 50% of their fruits per inflorescence (fig. 1). Thus, locating oviposition places at low densities seems a minor problem for female *Eurytonla* wasps and, consequently, overall inflorescence abundance is probably quite immaterial in this respect. The highly significant dependence of fruit predation intensity on plant identity (table I), on the other hand, was likely to be due to host-selection processes based on unknown plant traits, which might range from the chemical idiosyncrasy of individual shrubs to their spatial location.

As for any flowering plant, final fruit-set in *L. stoechas* results from a variety of factors including pollinator activity, plant physiological limitations, as well as the action of flower and fruit predators (STEPHENSON, 1981). Pollen limitations, however, probably make a minor contribution to final fruit set in this species since it is fully self-compatible (MuNoz & DEVESA, 1987) and high rates of pollinator visitation are a rule (HERRERA, 1988, and unpublished data). Furthermore, and since individuals lived close to each other on a sandy, apparently homogeneous site, we could reasonably assume that resource limitations were similar to all study plants. Thus, only flower and fruit predation would remain as major factors determining fecundity.

On the previous argument, final fruit set in *L. stoechas* would in fact ensue from a combination of flower and fruit predation intensities (note how average fruit set and percent flower predation of inflorescences correlate inversely; fig. 1), which in turn depend primarily on within-plant phenological variations. In contrast, plant identity or among-plant phenological variations affect fruit set only moderately. In other words, individual-specific traits which would potentially increase fecundity (e.g., flowering earlier, deterring predators more effectively through chemical protection) can become "diluted" into extensive within-plant variation. In conclusion, and even if the observed pattern of flower and fruit predation in *L. stoechas* was consistent through the years, the ability of predators to select against *L. stoechas*'s current phenology would probably be quite low.

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Acknowledgments

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Figure 1: Relation flowering phenology and flower-fruit predation

Table 1: Flowers and fruits preyed