

BRUCHUS AFFINIS AND THE FLOWERS OF LATHYRUS LATIFOLIUS: AN EXAMPLE OF THE COMPLEXITY OF RELATIONS BETWEEN PLANTS AND PHYTOPHAGOUS INSECTS

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Since Ehrlich & Raven (1964) introduced the concept of coevolution, phytophagous insects have been used to demonstrate mechanisms of coadaptation between plants and insects. G. Fraenkel (1959) had already stated that the "raison d'être of secondary plant substances" is an adaptation of plants to the attacks of insects. In most of the studies on this matter, attention is paid to the consumption of the plant tissues by insect larvae. Relationships between the adults of *Bruchus affinis* Frölich (Col. Bruchidae) and *Lathyrus* spp. (Leguminosae) prove that the mechanisms involved can be much more complex.

Lathyrus latifolius is a perennial semi-herbaceous vine which propagates by stolons. Pollination is by insects and the breeding system is essentially allogamous. Flowering and production of pods last three months (July, August and September) in the northern part of Béarn, France.

Bruchus affinis is a univoltin species. Adults emerge from pupae at the end of summer and live about 11 months, but they do not reproduce until they have undergone a reproductive diapause of nine months. Sexual activity and vitellogenesis do not start until the end of spring. At the beginning of summer, the females stick several isolated eggs on the young, green smooth pods of *L. latifolius*, *L. sylvestris* and *L. tuberosus*.

On hatching, larvae bore into the pods and then into the young seeds. As soon as the cotyledons have started growing, only one larva completes its development in each seed, after the elimination of the others. At the end of summer, after the dehiscence of the mature pods, a maximum of one adult emerges from each seed (Fig. 1).

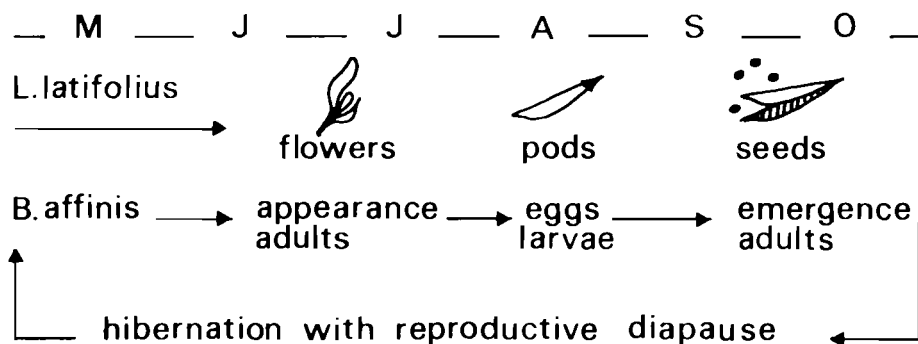


Fig. 1. Life cycle of *B. affinis* in relation to *L. latifolius*.

They show immediate activity; their fat body is whitish and very large while gonads are poorly developed. Although there are many adults emerging from the seeds, it becomes rapidly impossible to observe them on the late flowers of *L. latifolius* or on other flowers of the same colour. Adults emerging from seeds, kept in the laboratory, and confined with flowers of *L. latifolius* are not attracted to them.

A few adults were collected in winter under the bark of trees, near the populations of *Lathyrus*. Nevertheless, places where the adults gather during winter might exist. The bruchid numbers seem to be little reduced during the long period of reproductive diapause.

At the end of May, in Béarn, adults can be easily observed, for they visit the yellow flowers of *L. pratensis* in the neighbourhood of populations of *L. latifolius*. Their mouth parts are often covered with pollen. We have never found them feeding on the flowers of other plants.

Most of the adults collected in June on the flowers of *L. latifolius* have a large fat body. On the other hand, adults kept in cages outdoors, and fed with water and honey, have used all their reserves. Others, confined in petri dishes at 4°C ($\pm 1^\circ\text{C}$) still have a fat body similar to the one at the end of their larval development. Transferred to the outside temperature, they consume it rapidly.

Females of the adult stock and kept at 4°C, have been fed for more than one month with pollen of *Vicia sativa* and *L. pratensis*. Among the females fed with the pollen of *L. pratensis*, 15 of 22 showed pollen grains in their digestive tube and some of them (9/22) a whitish and abundant fat body. In the second experiment, the females fed with *V. sativa* showed no pollen grains and no fat body. Although they were confined with males, none of them were inseminated whatever the experiment (Bashar et al., 1985).

As soon as the flowers of *L. latifolius* appear, *B. affinis* adults leave the flowers of *L. pratensis* to reach those of *L. latifolius* (Fig. 2). One week after this move, some of the females collected in the field (6/15) contain mature ovocytes, a yellowish and abundant fat body, and they are inseminated. In the laboratory as well, females confined with males on *L. latifolius* flowers are inseminated, have an abundant yellowish fat body and ovocytes in retention (9 to 23 depending on the individual) (Table 1).

Expt.	number of <i>B.affinis</i>	duration in days	pollen in digestive tube	fat body	sperm in	ovocyte per female retention	per female vitello
	♀	-		-	♂	-	-
labo	10	14	+++	yellow	+++	14,6 ±3.8	18.1 ±4.2
field	15	9	+++	yellow	+++	4.3 ±2	10 ±3.2

During the day, adults fly over populations of *Lathyrus* and direct themselves towards the flowers, on which they land frequently. On the other hand, they land indifferently on any vegetative structure of any plant in the site. They walk about on the mass of vegetation and seem to find the green pods of *Lathyrus* at random. Once a suitable pod is located the female explores it carefully before sticking on her eggs.

Therefore, the flower is the only structure capable of attracting bruchids to the plant and is attractive even before anthesis, and through the color changes during the flowering period. The nature of this attraction is unknown; chromatographic methods have revealed no terpenes.

B. affinis adults get into the flowers, while they are still green and closed, by opening the standard. In well opened flowers, adults can be observed deeply settled into the corolla and others opening the anthers.

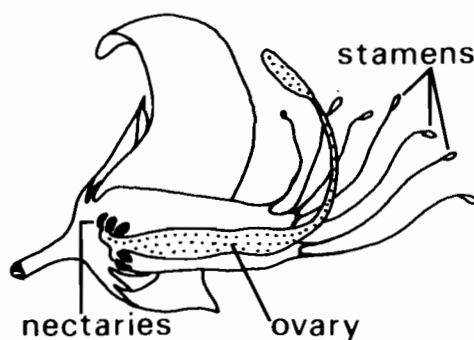
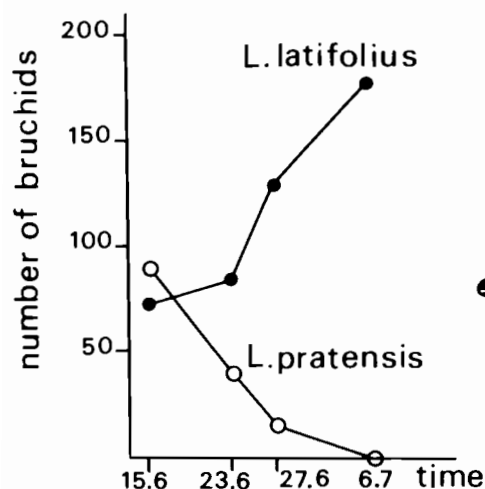


Figure 3. Cross section of a young mature flower of *L. latifolius*.

Figure 2. Displacement of *B. affinis* adults from *L. pratensis* to *L. latifolius*.

The flowers of *Lathyrus* have a ring of nectaries at the base of the staminal column, around the ovary (Fig. 3). Nectar has been collected, five times a day, at different dates, from flowers at different stages of development (unfortunately the damage done to the flowers does not allow the use of the same flower for several nectar collections). Nectar production starts before the opening of the flowers and soon becomes copious. Rate of nectar secretion and sugar concentration, both vary significantly with time of day and among inflorescences and plants (Hossaert et al., 1985).

The flowers are visited by *B. affinis* with a high frequency. In a *Lathyrus* population with a low density of *B. affinis*, two observers have followed, during 12h of a sunny day, (12.07.85, from 06h00 to 19h30 GMT with a break between 11h45 and 13h00, 44° lat.north-0° long day time from 04h34 to 19h40) the movements of the adults on 20 inflorescences (Table II).

For the duration of 10h15 of observation time, we recorded about 5 visits of *B. affinis* per inflorescence. The first visits occurred about 08h00. After 21h30, landings on flowers are not followed by new take-offs.

Just before nightfall, adults get into the flowers and remain there over night, one or several per flower; no movement of bruchids is recorded

Table II.

observation period	duration	No.landings observed	No B.affinis /h
8 am - 11.45am 1pm - 3.45pm	5 h 45	41	7.1
3pm - 7.30pm	4 h 30	65	14.4
total	10 h 15	106	10.3

during the night. When the weather is clear, flowers open within one hour after sunrise and, less than one hour later, **B. affinis** adults take off from the keel of the flowers. When the weather is cloudy, very few take-offs are recorded (Table III).

Table III. Observations on 20 inflorescences, 12.7.1985.

Night flights	take-offs before 08h00	diurnal visits	evening landings.
0	5	106	4

The number of adults reaching the flowers in the evening is similar to the number of adults escaping from them in the morning. This number is much lower than the number of the visits to flowers during the day. Two hypotheses can be proposed to explain these data:

a) if the adults visiting the flowers during the day and coming back to the same flowers to spend the night are the same; then the five residents observed previously would each make, on average, 20 visits during that time. According to this hypothesis, the same inflorescences would be used equally for resting and for feeding.

b) diurnal visits and nocturnal rests are independent with respect to the flowers. Some flowers would be used for resting and others for feeding.

The first hypothesis seems to be more likely, since independently conducted observations of adult behaviour, show that flowers are visited twice per hour.

This foraging activity of **B. affinis** adults on flowers of **L. latifolius** might have important consequences on the transportation and germination of the pollen, and on the fertilization of ovules as well.

Anthesis takes place two to three days before the stigma is receptive. After the opening of the anthers, the pollen grains fall down into the keel where they accumulate, but they remain able to germinate for five days. Therefore, the autopollen can be transferred to the stigma by insects moving about within the flower. Germination is then possible provided the surface of the stigma has been disturbed. The larger and more frequent are the insects, the greater the ease of penetration of the pollen into the style. Experimental manipulations have shown that repetitive intervention make the penetration easier (Valero et al., 1986). This seems to be necessary when there is no allopollen.

B. affinis not only can contribute to the transport of pollen to the flowers of this allogamous plant, it can also facilitate autogamy by moving

into the flowers when searching for pollen or nectar or sleeping inside the flower.

When visiting the flowers of *L. latifolius*, the adults of *B. affinis* can have effects on pollination at three different levels: stigmatic receptivity; transfer of autopollen from the bottom of the keel to the stigma; and bringing of allopollen. This "bringing" may not be uniform: the longer the bruchid stays in one flower, the higher the probability of its carrying pollen grains out of this flower: and we do not know if the same adults come back to the same flowers several successive nights and if the nectar of certain flowers is preferred to that of others.

One cannot forget that thrips stay in flowers as well and that numerous hymenoptera visit them. During the field observation, mentioned above, 137 visits of hymenoptera were recorded against 106 of the bruchid. But what is worth considering, is the narrow specialization of the trophic relationship between the adults of *B. affinis* and the flowers of *L. latifolius*. Only the flowers of three species of *Lathyrus* (*L. latifolius*, *L. sylvestris*, *L. tuberosus*) are capable of stimulating the gametogenesis of *B. affinis*. This specialization can be a contribution to the reproduction of these species.

At a first glance, it seems that *B. affinis* profits to the *Lathyrus* and conversely that, of course, *Lathyrus* entertains *B. affinis*.

Before concluding that a new example of coevolution exists between plants and insects, one must not forget that bruchid larvae are the only insects able to feed on the growing seeds and that in certain locations, 90% of them can be destroyed in such a way. Consequently it seems necessary to put the question: what is the importance of increasing the pollination efficiency in a plant species that reproduces also by stolons?

Before drawing any conclusion on the adaptative value of the attractiveness of the flowers for the bruchids, it is necessary to stress the importance of the relationships between the two species, and by viewing this in context to the ecological requirements of these two elements of the biotic community.

Finally, if one wishes to avoid seeing an adaptative advantage in every trait of the behaviour of an insect, it is necessary to recognise, as did Jacob (1981), that no adaptation can be perfect because it is a result of "tinkering" imposed by historical constraints. This "panglossism", using the term of Gould & Lewontin (1979), can only obscure our judgment and bias any attempt of analysis.

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