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The Co-operation Between the Asymmetric Flower of *Lathyrus latifolius* (Fabaceae-Vicieae) and its Visitors

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With 10 Figures

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Key words: *Fabaceae*, *Lathyrus latifolius*, *Leguminosae*. – Asymmetry, brush mechanism, flower ecology, morphology, secondary pollen presentation. – Hymenoptera, Anthophoridae, *Xylocopa violacea*; Megachilidae, *Megachile ericetorum*.

Summary

WESTERKAMP C. 1993. The co-operation between the asymmetric flower of *Lathyrus latifolius* (Fabaceae-Vicieae) and its visitors. – *Phyton* (Horn, Austria) 33 (1): 121–137, 10 figures. – English with German summary.

The flower of *Lathyrus latifolius* L. is strongly transformed by asymmetry. Legitimate visitors are forced into a position on the left wing by guiding structures. Thus the style is enabled to pass the bee on the right side. The flattened distal part of the style is twisted by some 90° to the left. The stigma at its tip touches the visitor first. Next follows the pollen-containing stylar brush which places an aliquot of its load onto the bee. A considerable strength is needed to trigger the flower. Main visitors and pollinators are females of *Megachile ericetorum*. Other megachilids as well as *Xylocopa violacea* do also visit this flower legitimately while *Apis mellifera* is totally incapable of working it.

Zusammenfassung

WESTERKAMP C. 1993. Das Zusammenwirken zwischen der asymmetrischen Blüte von *Lathyrus latifolius* (Fabaceae-Vicieae) und ihren Besuchern. – *Phyton* (Horn, Austria) 33 (1): 121–137, 10 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Die Blüte von *Lathyrus latifolius* L. ist stark asymmetrisch überformt. Legitime Besucher werden durch Leitstrukturen in eine Position auf dem linken Flügel

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gezwungen. Dadurch kann der Griffel die Biene rechts passieren. Die flächige Griffelspitze ist um 90° nach links gedreht und trägt an ihrer Spitze die Narbe, die bei dieser Passage den Besucher zuerst berührt. Darunter folgt eine Griffelbürste, die den Pollen enthält und der Biene portioniert anstreicht. Das Auslösen der Blüte erfordert sehr viel Kraft. Hauptbesucher und -Bestäuber sind Weibchen von *Megachile ericetorum*. Aber auch andere Megachiliden und *Xylocopa violacea* können im Gegensatz zu *Apis mellifera* die Blüte legitim besuchen.

1. Introduction

Floral symmetries are usually divided into actinomorphic and zygomorphic, with asymmetry reputedly extremely rare. *Fabaceae* although often serving as a typical model of zygomorphy contain several unrelated groups producing asymmetrical flowers. This is more widespread than hitherto suspected and reaches extremes in, e. g., *Phaseolus* (e. g., TROLL 1951), *Swainsonia procumbens* (WOOLCOCK & WOOLCOCK n. d.), and *Bolusia resupinata* (POLHILL 1976) with spirally coiled carinas. Two sections of *Lathyrus* are characterized by asymmetrical flowers (KUPICHA 1983). The genus is further distinguished by secondary pollen presentation, the style taking over the function of the stamens exposing pollen in a subapical brush, thus representing a pseudo-stamen. In this way, pollen donation and pollen reception are concentrated at the same spot in floral space, presumably a means which facilitates asymmetrical functioning of the flower. A pleurotribic pollen deposition is often combined with a brush mechanism of secondary pollen-presentation in *Fabaceae* (see also LAVIN & DELGADO 1990).

2. Material and Methods

The observations were made in the Botanical Gardens of Berlin-Dahlem and Mainz and in the environs of Heidelberg (Neuenheim: near the Zoo; Handschuhsheim: Gewanne Entensee and Höllenbach) in Germany. The bee species recognized as visitors at the specific localities were:

Berlin-Dahlem: *Megachile ericetorum* LEPELETIER, *M. willughbiella* (KIRBY), *M. circumcincta* (KIRBY), *Osmia tridentata* DUFOUR & PERRIS, *Bombus* sp. div., *Apis mellifera* LINNAEUS.

Mainz: *Megachile ericetorum*.

Heidelberg: *Megachile ericetorum*, *M. willughbiella*, *Xylocopa violacea* (LINNAEUS), *Bombus* sp. div., *Apis mellifera*.

In order to not destroy the small bee populations some few specimens were caught only. They are housed in the author's collection.

Field observations were supported by enlarging devices and a voice recorder. Photographs were taken using a 100 mm macrolens, a teleconverter (2×) and a flashlight. In the lab, I used a WILD-M5 dissecting microscope with a drawing tube.

The strength required by the bees to work the flowers was measured with a spring balance (max. 0.1 N) connected to wire-made adapters via a silky thread and a pulley. The adapter usually employed was a wide ring laid over the proximal part of

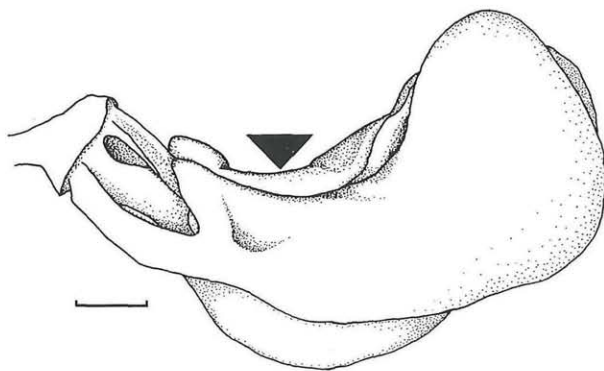


Fig. 1. *Lathyrus latifolius*. Wing-keel complex (calyx and vexillum removed) displaying the "centre of pressure" (arrow head). – Scale bar = 3 mm.

the alae-carina-complex (the "centre of pressure", see below and Fig. 1). The functioning of the flower and the scale of the balance then had to be followed simultaneously.

The presence of nectar was proven using Glucotest-strips (Boehringer, Mannheim) indicating glucose. Stigmatic activity was tested by the H_2O_2 -method (ZEISLER 1938).

The terminology to describe the position in floral space (right, left, above, below) refers to the view of a flower visitor and thus that of an observer which in fabaceous flowers normally equals the position in the floral diagram (see also TEPPNER 1990).

3. Floral Morphology

Floral morphology in *Lathyrus latifolius* L. is that of a typical fabaceous flower strongly transformed by asymmetry (Fig. 3). Most flowers are purplish-violet in colour but white forms with a pink tinge also exist. The standard bears a basal yellowish-white nectar guide accentuated by a more intense purple hue surrounding it. The darker purplish veins converge into the white spot. The carina is pale green.

The calyx is two-labiate, spaceous and slightly succulent, but does not play any role in floral function. A bulging of its upper side is indicative of nectar and related access holes (see below) inside, as in other nectariferous *Fabaceae*. The large vexillum is erect, flat and much wider than tall (ca. 32.5 mm vs. ca. 17.5 mm). The median runs in a fold ending in an apical indentation while the rim of the standard is lightly pulled forward. Its claw is conspicuously wide and covers about half of the flower's base. The lower parts of the standard, including the claw, are strongly asymmetrical (Fig. 3). Instead of the strong folds just above the wings in other *Lathyrus* species (e. g., *L. japonicus*, *L. pratensis*, *L. linifolius*) *L. latifolius* displays only slight protrusions in its claw.

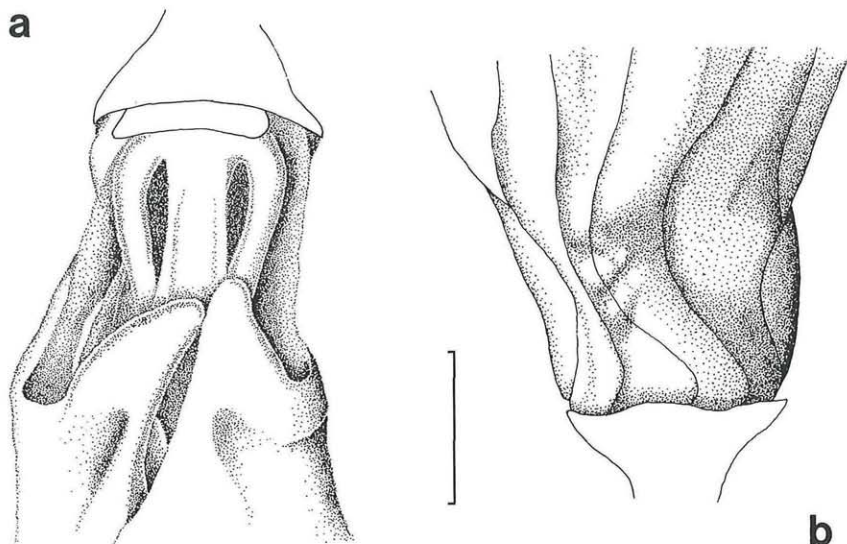


Fig. 2. *Lathyrus latifolius*. Details of flower base. – a) From above. From top to bottom: Receptaculum, scar of removed vexillum, filamental furrow and vexillar stamen with access holes in between, wing bases with auricles deflected to the right. – b) From below. S-like curvature of keel and wing claws. – Scale bar = 3 mm.

The alae are bent up banana-like and their rims curved inwards thus forming cucullate organs enveloping the keel. Just in front of the vexillar blade, the right wing overlaps the left (for definitions, see under Material and Methods) one including the upper edges of the keel into the leftward fold, while the left ala overlaps the right near the apex (Fig. 3). The wings are conspicuously auricled, these auricles being strongly inflated. Due to their deflection to the right (Fig. 2a) the distance of their tips to the insertion of their respective claws differs greatly: ca. 2 mm on the left, ca. 1 mm on the right. Distally of the auricles, each wing is furnished with a vaulting, the left of which is more pronounced than the right. Each of these thickened vaultings fits into a similar but more shallow depression of the keel. The petals are connected superficially to each other in this spot, the fusion being so strong that it is impossible to detach the leaves from each other without tearing out keel tissue. After a second vaulting a spoon-like cavity follows which houses the keel tip.

The carina is that part of the corolla most strongly transformed by asymmetry (Fig. 3). Its claws are curved s-like (Fig. 2b). The proximal part of the keel is bent to the right, its tip transcends the midline of the flower to the left. While the central column describes a u-shaped curve, the upper rim of the keel forms a secant to it. The keel-tip bulges on the left side above the stylar brush/pollen; accented by a strong inward fold on its

proximal side it almost forms a chimney which guides the style when the flower is worked by a visitor. A similar swelling is lacking on the right side.

Basally, the androecium begins as a tube and then divides into a filamental furrow and the wide vexillary (i. e., median upper) stamen giving access to the nectar chamber by way of two wide openings in between. These openings or "fenestrae" do not represent simple gaps between filaments, but instead are proper orifices giving access to the nectar chamber. Distally, the parts form a false tube, the winged vexillary stamen being tightly appressed to the furrow. The filaments composing the furrow may be distinguished spatially. The widened basal part of the staminal tube forms a large nectar chamber which of course is never quite filled by nectar. The access holes on either side of the vexillary filament are of different relative dimensions, in the extreme (each) one of them could even be closed. The receptacle is widened into a 4 mm wide shallow hypanthium bearing the low nectarial disc. This intrastaminal disc is as discontinuous as the filamental tube: it consists of a u-shaped lower portion in front of the furrow and a single protuberance opposite the vexillary stamen. Although no asymmetry is obvious in the disc, the nectar droplet is often found below the right(!) access hole only. A glucose test was positive, the solution in some cases being too concentrated to be imbibed by the paper.

The free parts of the filaments are threadlike but slightly swollen just below the punctiform insertions of the anthers. There are two levels of anthers, an outer whorl (including the carinal stamen) representing the upper storey, and an inner whorl (including the vexillary stamen) forming the lower one. Dehiscence has already occurred when anthesis begins. Most pollen resides within the stylar brush with only few grains reaching the naked back of the style. The median line of the rear side and the stigma remain free of pollen (herkogamy).

The gynoecium starts with a short gynophore. The ovary is pubescent over most of its length, only becoming glabrous when it narrows into the style. Besides the pollen-presenting brush the style remains naked. The ovary runs straight and the style describes an upward curve forming a wide „U“. Like the keel, the proximal part is bent to the right and the tip transcends the plane of symmetry to the left. Moreover, the distal third of the style is twisted by some 90°, the adaxial brush thus facing to the left. The brush-carrying plate is widened and flat, while its rear side is convex and glabrous (Fig. 4, 5).

The style is terminated by a widely conical (adaxial) stigmatic flap on the same side as the brush (Fig. 5, 6). The H_2O_2 test revealed that the stigmatic zone was situated on its distal side, the proximal side did not show any reaction. Even the active zone reacted only after scratching its surface (= destruction of the pellicula?) (The reaction of pollen to the H_2O_2 was much stronger than that of the stigma).

The stylar brush (Fig. 5, 6) begins with two rows of erect hairs forming a fence at the rim of the style, just below the stigmatic flap. It is followed by an all-surface brush of erect hairs and ends again in two rows of hairs. The entire brush works as a pollen-presenter containing all pollen between its hairs. This kind of secondary pollen presentation in which the style acts as a stalked stamen offering pollen in a restricted space has been termed pseudo-stamen (WESTERKAMP 1989).

4. Floral Development

Floral development has been described in some detail by SCHÜEPP 1911. Thus, only some additions relating to asymmetry are needed here. Asymmetry in *Lathyrus* is the result of growth processes occurring late in ontogeny. In a bud (6–7 mm in length) in which the calyx still totally embraces the flower no traces of asymmetry can be detected. The calyx teeth are positioned in an ascending cochlear manner. The peripheral fusion of the vexillum around the remainder of the flower is only in its initial phase at the tip of the leaf. The rows of papillae serving this closure (SCHÜEPP 1911), however, are already available further down. The extent of fusion increases until the flower opens. The style is straight and oriented horizontally in a bud of 8 mm, its tip, however, shows first signs of a slight turn to the left.

At a bud length of 14 mm, the vexillum is totally fused below the remainder of the flower. Neither wing nor keel petals show any indications of asymmetry at this stage. The tip of the style has already turned by some 90°. The entrances to the nectar chamber can be distinguished but are hidden below the vexillar stamen.

A bud of 17 mm gives first hints of asymmetry in the petals. The s-like curvature of the keel and wing claws is indicated from below, while the upper rims of the wing-keel-complex basally begin to overlap to the left. The wing and keel petals are fused inside the ball-socket-joints to such an extent that they cannot be separated without tearing out some keel tissue.

Fig. 3. *Lathyrus latifolius*. Flower from below displaying strong asymmetry.

Fig. 4–6. *Megachile ericetorum* at *Lathyrus latifolius*. Notice scratch-marks on the wings. – Fig. 4. Male. The pollen-presenter does not contact the bee while passing over. – Fig. 5. Female. Pollen-presenter overtopping the bee. The stigma is covered with pollen. Notice inflated auricle of right wing which guides the proboscis. – Fig. 6. Female. The pollen-presenter has forced the wings apart. The stylar brush is emptied while the stigma is pollinated.

Fig. 7–10. *Xylocopa violacea* at *Lathyrus latifolius*. – Fig. 7. Female, perching amidst the flower. Notice tibial spurs. – Fig. 8, 9. Female, embraced in the neck by the pollen-presenter. – Fig. 10. Female displaying the semicircular pollen-filled stipital comb at the base of the proboscis. Notice the pollen load at the front of the thorax.



The keel shows some asymmetry but its tip is still symmetrical. The style has begun to bend upward.

5. Floral Kinetics

An insect's visit to a flower starts with the insertion of the proboscis below the vexillar guide mark for which visitors have to overcome the resistance of the two closely fitting auricles (Fig. 2a) of the wings which obstruct access to the nectar. These auricles, together with the guiding track on the lower side of the vexillar claw adjust the proboscis toward the right access hole (Fig. 2a) and force the bee into a position suitable for the functioning of the flower. The proboscis insertion is facilitated by an initial downward-pressing of the wing-keel-complex just in front of the flag ("centre of pressure" below, Fig. 1) because this results in an opening of the tongue channel between the auricles: Since the basal pit which connects the left wing and keel petals originally lies above the central column it is moved leftward when the ala is pressed downward. This leads to a leftward movement of the left auricle, too, and thus opens the tongue channel. If the right half moves at all, it does so only downward, perhaps including a minute sideward motion as the wing-tip is guided by the outward curve of style and keel. Because the basal pit is already situated besides the column, its movement does not have any comparable opening effect. It is not evident if the initial lowering of the wing-keel-complex facilitates proboscis-insertion or if the thrusting in of the tongue facilitates the sinking of the carina. In any case, the depression of the left wing allows the lowering of the keel and an opening of its upper rim thus facilitating the protrusion of the pseudo-stamen. A thrust onto the centre of pressure makes the right wing move downward only while the left ala is rotated from the originally vertical to an horizontal position in the pivot of the ball-socket-joint, the more it is lowered the more horizontal it becomes (compare left and right wing in Fig. 4). The left wing often is moved until meeting the standard while its right counterpart is hardly moved horizontally. The thrusting of the forehead against the lower side of the standard claw leads to a strain of the thoracic venter onto the centre of pressure. The force is produced by the legs which push (hindlegs, inserted at the wing tips) and pull (fore- and midlegs, inserting at or just distally of the proximal pit) the bee into the flower. At the point of pressure the way the wing-keel-complex has to be pushed down is least. This way is much longer if one tries to produce the same effect by handling the left wing tip only.

To work fresh flowers by hand, a force of ca. 0.1 N is needed at the centre of pressure (Fig. 1). Taking into consideration the distance of 7 mm from the centre of rotation, a moment of rotation of $7 \cdot 10^{-4}$ Nm results. The weights of the bees measured (one specimen of each species only) were: *Megachile ericetorum* female: 0.0845 g; *M. ericetorum* male: 0.07 g;

Xylocopa violacea female: 0.736 g. Calculating with the weight of the *M. ericetorum* male, a lever arm of ca. 1 m in length would result if he tried to trip *L. latifolius* flowers by weight alone. At the centre of pressure, on the other hand, the bee would need a weight of ca. 10 g to work the flower. Applying this weight to a flower, however, would result in a dangling of the entire flower and not in an opening of the angle between the vexillar claw and the wing-keel-complex. As the forces are applied by driving in a wedge between the standard and the wing-keel-complex, smaller but vigorous bees are also able to work these flowers.

The bees' tarsal claws and tibial spurs often leave considerable scratchmarks behind (Fig. 4–8), those of the claws in the alar surfaces, those of the spurs at the upper rims where they often catch the wing (Fig. 4).

While the wing-keel-complex is moved downward, the pollen-presenter remains in its original position. Stigma and stylar brush thus perform an upward movement relative to the bee. During this sweep the stigma first (!, herkogamy!) contacts the – eventually pollen-laden – flank of the bee. The stylar brush then affixes (further) pollen to it. Finally the sexual sphere of the pollen-presenter overtops the bee (Fig. 6). The pseudostamen appearing to the right of the bee prevents a movement of its body including the right hindlegs toward that side. When the visitor withdraws from the flower another aliquot of the pollen is delivered to the bee. As contact of the pseudostamen to the bee is short in most cases (for an exception see below) this results in an increasing of male fitness by a portioning of the pollen available.

As long as the left wing overlaps the right one at its tip, a downward movement of the wing-keel-complex is hardly possible and access to the nectar is thus blocked. The forces needed to overpower the style which is still included are too great for most bees.

In contrast, TEPPNER 1988 who has investigated flowers of *L. grandiflorus*, *L. tuberosus* and *undulatus* (and *L. latifolius*, personal communication), and *Xylocopa violacea* and *Megachile ericetorum* (and *M. willughbiella*) respectively, is of the opinion that the two halves of the wing-keel-complex behave mechanically different, the right half being easier to press down than the left one; the simultaneous downward movement of the right wing auricle should open the access to the nectar and the bees should learn to use the easier access at the right half for exploiting the flowers.

6. The Insect Visitors

6. 1. *Megachile ericetorum* (Megachilidae) (Fig. 4–6)

Wherever observations have been made, *M. ericetorum* is the most frequent visitor and pollinator. Most data given in the chapter on floral kinetics refer to this species and do not need to be repeated here. While

striving for nectar the bee slowly sinks into the flower between the two wings or perches on the left wing. The sinking is sometimes intensified by a bending of the wasp-waist of Megachile leading to a rise of the metasoma relative to the thorax. An actual raising of the metasoma which is sometimes thought to typify megachilid bees (see WESTERKAMP 1979) is only observed in females visiting *L. latifolius* when defending males patrolling the flowers in search of mates or rivals. Meanwhile the stigma touches the bee's right side whereafter the pollen laden stylar brush places pollen onto the insect. Finally the pollen-presenter overtops her by some amount (Fig. 6). The region where the bee's flank is hit by the pseudo-stamen depends on the size of the flower and the depth the bee has already reached in her way to the nectar. The pollen-dusted part may lie between the middle of the thorax and the second abdominal segment. Sometimes the style rises between the two wings forcing them apart (Fig. 6) and smearing them with pollen on both sides, thus creating serious problems for the bee when she tries to take wing afterwards.

The duration of nectar drinking varies widely: from an alluded sip to more than a minute, 10–15 sec. being typical. Licking movements of the labium and pumping of the metasoma can be seen. These movements were of no concern for pollen uptake as the pollen-presenter widely overtopped the bee during drinking. Contact between the bee and the sexual sphere of the pseudo-stamen takes place only in the initial phase of the visit and when the bee leaves the flower.

The great efforts needed to enter the flower mostly distract the bees from the contact with the sexual sphere but sometimes they appear unpleasantly struck by the pressure exerted by the pollen-presenter. They then try to keep it off their bodies which results in a dusting of the right foreleg. It remains unclear if it is the lateral touch which irritates her or if it is the contamination by the pollen that makes her uncomfortable. Rarely, bees tried to reach the nectar from the right wing and to escape whatever touch. On the other hand, bees often do not pay attention to pollen sticking to their flank. Pollen is groomed off every now and then, but this imperfectly, especially above the tegula. Therefore, sufficient pollen grains for pollination of all further flowers remain in spite of the grooming attempts. Often the brushing process is one-sided only and restricted to the right midleg because of the asymmetry of pollen application.

L. latifolius is a nectar flower, adapted in its function to nectar searching bees, and foraging for pollen has to be dealt with separately. *L. latifolius* does not offer surplus pollen which is thus taken from the quantity provided for pollination. Pollen is hidden in the flower and remains invisible to visitors during foraging.

The process of pollen uptake begins at or near the end of nectar drinking. The bee raises her waist which results in a withdrawal of the

exserted pseudo-stamen into the keel. If the bee does not act fast enough the pollen-presenter may escape and disappear within the carina. Normally, she first tries to attach her ventral scopa to the stylar brush. In this way some pollen is taken up directly into the right half of the scopa. The raising of the wasp-waist then goes on as does the turning of the bee initiated when moving the scopa against the stylar brush. Finally, she sits rectangularly across the wing-keel-complex, the metasoma lying behind the style, the scopa adjacent to the naked rear of the pollen-presenter. In the meanwhile already, mid- and hindlegs brush the style. At first, the right (esp. hind-)legs often do not get hold of pollen as they touch only the naked rear side of the pollen-presenter. Just before or soon after taking wing pollen is reloaded from the legs to the ventral brush. The midlegs are pulled through the hind basitarsal brushes which are pushed against each other. Subsequently the hindlegs are rubbed together as if the insect strives for an equipartition within the scopa. Sometimes bees even scrape pollen off the scopa which was deposited asymmetrically by direct uptake from the pseudo-stamen. Finally, pollen is transferred to the metasomal ventral scopa by moving the hindlegs anteriorly while keeping the inner face of the basitarsus attached. During this process the metasomal segments are spread open: gaps appear between the brushes of single segments ready to take up pollen. As more pollen accumulates within the scopa it is sometimes tapped to fasten it. After the reloading process the basitarsal brushes are free of pollen again (but see below) as is observed in a bee starting to visit the next flower.

On some occasions I had the impression that visits were pollen-only visits when bees made no attempts to reach the nectar. Sometimes they presumably not even exserted their proboscides but only thrust their heads beneath the standard to expose the pollen-presenter and then turned their scopa against the stylar brush.

Pollen gain is also possible after entering the flower from the right wing. During the withdrawal of the style its pollen-presenting part is grasped and groomed. In those cases nectar stealing is combined with pollen stealing.

After heavy rainfall pollen foraging is often delayed for some time. The bees then have considerable difficulties with the unaccustomed viscous pollen, large clumps of which sometimes fall to the ground.

Since I never saw *M. ericetorum* working a flower in a clumsy, inexperienced manner I suppose that these bees do not have to learn the handling of this flower individually. Pollen foraging especially is not accessible for learning as bees are unable to detect if a pollen-presenter still contains pollen. They often conduct all movements for pollen uptake with totally empty stylar brushes. The question of conscious control of pollen uptake remains an enigma. It remains also unclear whether the bees

are able to measure how far their scopa is filled or how large their foraging success is. Perhaps the amount of pollen already deposited in the cell under preparation is a measure for the bees' foraging success, and the fact that no more pollen can be transferred from the hindlegs to the ventral scopa could be an indicator for the bee to return to her nest. Pollen foragers of, e. g., *Osmia mocsaryi* always returned to the nest with pollen-laden hindbasitarsal brushes (WESTERKAMP 1987).

Nectar-only visits alternated with those in which pollen and nectar were harvested in an irregular manner. In the afternoons when most flowers were emptied of their pollen the bees relaxed in their efforts to collect pollen.

M. ericetorum did not avoid flowers visited recently and repeated visits to the same flower were sometimes observed. Occasionally blossoms were used which were in the last bud stage or already spent.

In spite of their smaller size males of *M. ericetorum* (Fig. 4) managed to exploit and trigger the flowers because they were forceful enough to press down the wing-keel-complex when perching in the right (left!) place. Stronger still than females they bent in their waist. However, they were so small that hardly any contact was accomplished between the bee and the sexual sphere of the flower (Fig. 4), sometimes however, it happened when they left the flower. Thus in general, males are able to pollinate the flowers. Perhaps they promote outcrossing in a different way: When trying to copulate with females, they often startle them to change to another inflorescence/plant. An actual copula was never observed as the pairs usually fell from the flower and escaped from the observer's sight.

6.2. *Megachile willughbiella* (Megachilidae)

This species was observed more rarely than the previous one. Females often visited the flowers illegitimately: they then landed on the right wing and entered the flower from this perch (finally reaching the left access hole?). When resorting to this method of visit the bee was briefly touched by the naked back of the pollen-presenter, which then owing to its inherent flexion turned off the bee. In some cases she even had to lift her metasoma to make the style pass by. It cannot be said to which extent this is a learned behaviour to escape the "unpleasant" contact with the contaminating pollen(-presenter).

Nevertheless the bees are able to visit the flowers legitimately also, partly alternating within a certain foraging bout. They have to make the greatest efforts to enter the flower and have to move to the far left to give way for the style on their right. Obviously, these females are too broad for this flower as compared to the previous species (thorax: 4.4 mm vs. 4.1 mm; metasoma 4.6 mm (!) vs. 3.8 mm). The pollen-presenting stylar brush may meet the bee's flank at different spots: in front of the wings, in between of

the wings, at metasoma segments 2 or 3. It may pass over the total width of the thorax.

Instead of their small dimensions the males of *M. willughbiella* no doubt are able to handle the flower legitimately. Contact (of metasoma segment 3) to the pseudo-stamen of course partly takes place only when leaving the flower. The males are strong enough to work the flower also from a median position which prevents the style to leave the wing-keel-complex.

6.3. *Megachile circumcincta* (Megachilidae)

Drinking nectar.

6.4. *Osmia tridentata* (Megachilidae)

A female in a legitimate visit pulled down the wing-keel-complex so far that she was widely overtopped by the style and finally reached a vertical position.

6.5. *Xylocopa violacea* (Anthophoridae) (Fig. 7–10)

First observations (end of June 1990) suggested that *X. violacea* is able to reach the nectar of *L. latifolius* but does not trigger the flower. The bees landed in the middle of the wing-keel-complex, a position not permitting the pseudo-stamen to emerge (Fig. 7). Thanks to their much stronger force they obviously were able to press down this complex including the style until they reached the nectar. Following observations three weeks later revealed that the bees had learnt to work the flowers in the proper way. Now they perched on the left wing, enabling the style to pass on their right side (Fig. 8, 9) brushing pollen onto them or taking over pollen delivered by the bees. Instead of *L. grandiflorus* where the pollen-presenter embraces *X. violacea* in the wasp-waist (TEPPNER 1988) it is hugging her in the neck in *L. latifolius* – shifted by just one tagma. It reaches the midline of the bee or shortly beyond, remaining in this position (Fig. 9) until the completion of the visit. The pseudo-stamen dusts the bee on the right back of her head but more so at the front of the thorax (Fig. 10) and at the right foreleg. Structures particularly of the wings guide – after a learning phase? – the strong proboscis to the nectar and thus the bee to a position which results in pollination. This holds good for males as well as females. The latter were also observed opening buds in advanced stage of development to – successfully – extract pollen.

Two ways of pollen uptake are apparent (for definitions, see WESTERKAMP, in prep.): For primary (direct) pollen foraging the bees lifted their waists and with their forelegs reached the pseudo-stamen. The first to get hold of it was the right foreleg which held the style off the bee and protruding from the keel. The two legs then groomed pollen from the stylar

brush. In secondary pollen uptake the bees every now and then brushed pollen off their contaminated right flank – aimed at harvesting it. Their grooming efforts were imperfect only with much pollen remaining in the incision between head and thorax and thus ready for pollination. Interestingly, there were two methods to proceed with the pollen gained in either way. The usual way was to pass it from the foreleg to the midleg and then to the ipsilateral hindleg where it accumulates in a voluminous scopa (to be found on basitarsus through tibia, contrary to the statement of FRIESE 1923: 194 that it is typically located on the basitarsus only) for homeward transport. Because of the one-sided pleurotribic pollen application the harvest mostly accumulates in the right hindleg scopa. Pollen transport on the hindlegs (basitarsus, tibia and femur) was already described by TEPPNER 1988 for the harvest on *L. grandiflorus* flowers. All this clearly demonstrates that xylocopas do transport considerable loads of pollen also externally and not more or less in the crop only as suggested by BISCHOFF 1927 and SCHREMMER 1972. A second method utilized was to pass pollen on in a forward direction, i. e., from the thorax-grooming midleg to the foreleg. This is contrary to the orthodox reloading direction of bees in which pollen is always worked backwards. It is thus an evolutionary innovation. Pollen then is scraped off the foreleg by a stipital comb (Fig. 10) and finally swallowed. Interestingly, this is done by both sexes alike. Therefore it cannot be a method solely for females which are said to transport pollen mainly in the crop (SCHREMMER 1972).

Females sometimes approached flowers but hesitated in front of them, at times touching them with some legs but without completely landing. The flowers avoided for some time in this manner had been visited just before by another *Xylocopa* female which obviously left a scent mark behind. None of the other bees including *Xylocopa* males seemed to perceive this stimulus, they never showed a similar avoiding reaction. Comparable observations were reported by FRANKIE & VINSON 1977 in *X. virginica texana*.

6.7. *Bombus terrestris* (Apidae)

Only rarely bumblebees of this species visited flowers legitimately. They then were able to trigger the flower. On most occasions, however, they approached the nectar between corolla and calyx, mostly (and then constantly) utilizing the gap between the claws of the standard and wing petals on the right (!) side. Their intense activity left lesions or tearings behind in the calyx rim between the lateral calyx teeth. The bees were never observed to puncture the flower.

6.8. *Bombus pascuorum* (Apidae)

Besides a multitude of attempts to work flowers illegitimately this species performed most legitimate visits I could observe in bumblebees. It

also had to work hard to reach the nectar. Most visitors were tiny specimens, their metasoma tip just reaching the left wing tip. The stylar brush mostly hit them at the level of the tegula or little behind. Before leaving the flowers they always with a forward stroke of the midlegs brushed pollen off the thorax which finally accumulated in large pellets in the hindleg corbiculae.

6.9. *Bombus* sp. (Apidae)

Either specimens concerned were too much spoilt for identification in the field, or the exact names are missing because of the poor taxonomic knowledge of the author when starting observations.

In addition to the behaviours already described with the two species of *Bombus*, these bumblebees sometimes tried to gain access to the pollen-presenting brush with their mouthparts. Often, I observed specimens biting an opening through calyx and claw of the standard to get access to the right (!) nectar hole. This biting was easily perceived because of the crack always accompanying it. Burglarizing ever happened in the very same spot! After puncturing the flower nectar (?) oozed out of the hole.

6.10. *Apis mellifera* (Apidae)

Honeybees were extremely rare at *L. latifolius*, even if several colonies were in close vicinity. Only once I counted >10 workers in a larger stand which obviously had been recruited here by mistake. Despite intense search I never observed a legitimate visit of a honeybee. They always behaved clumsy, aimless, unwitting where to look for what. Only as secondary robbers they acted purposefully. I had the impression that normally scouts only tried the flowers but never discovered the solution and thus $\pm$ never recruited to this species. Obviously this is a bee flower honeybees cannot handle for whatever reason!

6.11. Further visitors

Hoverflies (several spp.): gleaning pollen

Butterflies (several spp.): drinking nectar

7. Competition

In a certain garden two plots of *L. latifolius* supported by the southern and northern fences, respectively, were some 20 m apart. In spite of their proximity the bee faunas of their exterior faces differed greatly. The northern plot which was richer in flowers but only received glancing light at the time of pollen foraging was usually visited by 3-4 *Xylocopa violacea*, few bumblebees and a sporadic megachilid. The south on the other hand lay in the full sun and was poorer in flowers but visited by 10-

15 megachilids and no *Xylocopa*. In the absence of *Xylocopa* from the northern flowers the numbers of *Megachile* specimens increased while the carpenter bees came to the south if megachilids were rare or absent. The only competitive interactions observed were "attacks" (whether copulatory or "territorial"?) of *Megachile* males. They startled most other bees. Their peculiar females remained in their perches but often were pushed from the flowers. *Xylocopas* were irritated but went on drinking nectar. With increasing *Xylocopa*-number and decreasing quantity of flowers the carpenter bees became more and more hectic. *Bombus pascuorum* and *xylocopas* did not influence each other. All those bees left flowers when *Apis* was approaching. This even included *Xylocopa* as I could observe on several occasions. *Megachile ericetorum* on the other hand was dislodged even by approaching hoverflies.

As most bees did not show agonistic interactions it remains unclear if there exists some sort of pecking order within them – and what forms the basis for it. A positive effect of competitive interactions may have been that specimens were forced to fly some distance and perhaps to another plant thus shifting the ratio of geitonogamy and allogamy in favour of the latter.

8. Conclusions

Megachile ericetorum was the main visitor and leading pollinator in all localities. These were all outside the natural range of *Lathyrus latifolius*. But as the areas of both species widely overlap (HEYWOOD & BALL 1968, FRIESE 1895–1901) there are no objections against the idea of a long-time interaction of *M. ericetorum* and *L. latifolius*. A learning of the proper handling of the flower has never been observed in spite of the high complexity of the movements involved. The behaviour in the flowers was thus constant in time as in (my) localities that females of *M. ericetorum* may be considered the head pollinator of *L. latifolius*.

Obviously, *M. willughbiella* females are too wide for these flowers but do learn how to handle them successfully (and legitimately).

Xylocopa violacea is a long-lived insect and thus forced to be highly flexible. On the other hand, *L. latifolius* does not match the criteria for *Xylocopa*-flowers established by PIJL 1954. Nevertheless both sexes are able to acquire the proper handling and may thus pollinate *L. latifolius*. As the bee stays in close contact to the sexual sphere of the pseudo-stamen during the whole visit (Fig. 9), this leads to a (too?) rapid depletion of the pollen reservoir thus reducing the male fitness of the flower. This also contradicts to accept a role as adapted pollinator for *X. violacea* although pollen is located in a very safe place in this bee as compared to other species. *Bombus* females only rarely visit legitimately and are no reliable pollinators. *Apis*, however, is (totally?) incapable to work these flowers.

Interestingly, most visitors (legitimate as well as illegitimate) strive for the right access hole which might point to an asymmetrical nectar production.

To sum up, *Lathyrus latifolius* may be characterized as a pleurotribic bee-adapted nectar flower with asymmetrical guidance of the pollinator and a certain predestination for *Megachile ericetorum*.

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Recensio

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