

## Pollination biology of the Sea Pea, *Lathyrus japonicus*: floral characters and activity and flight patterns of bumblebees

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### Summary

The pollination biology of the circumpolar seashore plant *Lathyrus japonicus* WILLD. was studied in two populations in Denmark, 1991–1992, and in one population in northern Norway, 1991. The studied plant characters were flower fragrance, flower colour, nectar production, pollen, flower phenology, and pollen/ovule-ratio. The flowers smell faintly and aromatically and absorb UV light with the entire surface; within the blue waveband there are nectar guides. The flowers are purple and change colour to violet before wilting but nectar volumes remain largely unchanged. Each flower was open for 2–3 days in 1992 and for at least 6 days in 1991, the difference being due to draught in 1992. The ten stamens released all together 40,000–50,000 pollen grains which were deposited in the stylar brush and accumulated in the keel before the stigma became receptive. In spite of this protandry, the flowers are functionally homogamous because viable pollen is present at the time the stigma is receptive, which is only after rupture of the cuticle of the stigmatic papillae by, e.g., a bee. The average pollen/ovule-ratio was 6,384, assigning the flower to xenogamy according to the classification proposed by CRUDEN (1977).

*Lathyrus japonicus* is pollinated by several species of bumblebees (*Bombus* spp.) and one species of mason bee (*Osmia* sp.), a pollinator guild similar to that of many other species in the genus. The pollinator guilds of the two subspecies of *L. japonicus* (subsp. *japonicus* and subsp. *maritimus* (L.) P. W. BALL) were largely similar. *Bombus pascuorum*, the most important pollinator, flew longer distances between inflorescences than predicted from the nearest-neighbour-distances between inflorescences. *Bombus pascuorum* also visited just one flower per inflorescence more often than inferred from the number of flowers open in an inflorescence. On sunny days with no rain, each flower was visited by bumblebees on average 7 times per day, indicating abundant pollinators.

Key words: *Lathyrus japonicus*, *Bombus*, *Papilionoideae*, bumblebee flight pattern, pollination biology.

### Introduction

*Lathyrus* is typically bee pollinated. The flowers attract bees by colour, pattern, scent, pollen, and nectar. Little is known about the pollination and breeding systems of the 159 species belonging to *Lathyrus*. Only the following five species have been investigated until now: *L. tuberosus* (CHAIB et al. 1986), *L. sylvestris* (CHAIB et al. 1986), *L. latifolius* (CHAIB et al. 1986, HOSSAERT et al. 1986, VALERO et al. 1986b, WESTERKAMP m.s.), *L. grandiflorus* (TEPPNER 1988) and *L. odoratus* (e.g., JONES 1965). All belong to the advanced section *Lathyrus*, whereas *L. japonicus*, the subject of the present study, belongs to section *Orobus*, which is considered the most primitive section within the genus (BÄSSLER 1973, KUPICHA 1983).

According to "Flora Europaea" (BALL 1968) and "Flora

Nordica" (ASMUSSEN in prep.) there are two subspecies, subsp. *japonicus* and subsp. *maritimus* (L.) P. W. BALL, distinguished by differences in flower and fruit size. Animal pollinators such as bees can affect selection on floral characters if visitation behaviour and pollen transfer capability varies with floral phenotype (WASER 1983). For example, larger bees favour larger flowers, and a large flower is visited more often by large bees than by small ones. Thus, differences in flower size between populations of a plant species might be explained by differences in pollinator guilds, and it has been shown that floral differentiation among varieties can be correlated with distributions of specific pollinators (MILLER 1981, GALEN et al. 1987, GALEN 1989). One of the questions addressed by the

present study thus was whether the differences in flower size between the two subspecies of *L. japonicus* are evident also in their pollinator guilds.

Several characters of a plant may act as visual and olfactory stimuli and thereby affect the probability of pollination. Whether a bee discovers and is attracted to a flower is likely to depend on the density of flowers, smell, colour, nectar, pollen amount, and the presence of other flowering plants in the community (FÆGRI & VAN DER PIJL 1979, DAFNI 1992). After a pollen grain has become attached to the hairs of a bee, the probability that it will sire offspring depends on the flower constancy of the bee, the time between grooming events, the receptivity of the receiving stigma, and the viability of pollen.

Pollinators can be a limiting factor on sexual reproduction in a plant (BIERZYCHUDEK 1981). Thus, an individual flower's probability of being visited depends on the overall activity of the bees in the population; and it depends on the foraging behaviour of the bees. Between-patch-flights and within-patch-flights are important aspects of the behaviour of the pollinator, because it influences pollen flow distances, and are usually described by measures of the bee's flight distances, flight directions, and turning angles both between patches and between inflorescences (PYKE 1978, 1979, WADDINGTON & HEINRICH 1981; WADDINGTON

1983 for a summary of investigations). Frequency distributions of flight distances are always leptocurtic (PYKE 1978, ZIMMERMANN 1979, WADDINGTON 1981). Considering turning angle, pollinators either tend to fly in one direction (PYKE 1978; WADDINGTON 1980) or they change direction at random (e.g., ZIMMERMANN 1979). When approaching an inflorescence the pollinator decides which flower to begin at, which flower to visit afterwards, and how many flowers to visit before leaving for the next inflorescence. Optimal foraging theory predicts that pollinator movements are the result of natural selection for maximising net rate of energy intake while foraging (e.g., PYKE et al. 1977). For example, a bee pollinator searching for nectar should avoid revisitation of flowers (HEINRICH 1975), it should minimise expenditure of energy in moving between flowers and it should only visit flowers containing nectar.

Besides looking for differences in the pollinator guilds between the two subspecies of *L. japonicus*, this study therefore addressed the following questions: (1) which plant characters of *L. japonicus* are likely to affect the probability of pollination; (2) is the pollinator guild of *L. japonicus* similar to that of other *Lathyrus* species; and (3) how are the activity and flight patterns of the pollinating bumblebees related to flower distribution within a patch.

## Materials and methods

### Study sites

The main study site was Thorup Strand at the north-west coast of Jutland, Denmark (57° 08' N, 9° 07' E). At this site, *L. japonicus* was growing in dense but separated patches (in the present study the term patch refers to separately growing groups of *L. japonicus* with at least 4,000 flowers). The plants were growing behind and on the ridge of the outermost range of sand dunes. Observations were made during the flowering seasons 1991 and 1992. Supplementary data were collected in 1991 at Ajstrup Strand, Denmark (56° 03' N, 10° 15' E), and at Nordreisa beach in northern Norway (69° 50' N, 21° 04' E).

### The plant

*Lathyrus japonicus* is a circumpolar seashore plant in the northern temperate and Arctic zones. The habitats are sandy or gravelly seashores and sand dunes. *Lathyrus japonicus* is a long-lived perennial that reproduces vegetatively by long, slender rhizomes. Every ramet has several inflorescences with 4–10 flowers. The flowers are purple and change colour to violet before wilting. White-flowered individuals occur rarely at several localities in Denmark. The flower is a symmetrical pea flower with a rather large standard (18–23 × 12–18 mm). Nectar is secreted from a nectary on the inner surface of the floral receptacle between the staminal tube and the ovary. The stamens are diadelphous (i.e., the vexillary stamen is free and the other nine are fused together in a staminal furrow), and bees suck nectar through two access

holes at the base of the upper stamen. During bud stage pollen is deposited in a stylar brush at the adaxial side of the style. Flowering seasons in the Nordic countries range from the end of May to the end of August; the population at Thorup Strand flowers in June. The fruit is a pod containing 3–9 seeds. The pod is dehiscent and the seeds are dispersed secondarily by sea currents (RIDLEY 1930) or by doves (BRIGHTMORE & WHITE 1963).

### Plant characters affecting pollination

**Fragrance.** Fragrance of the individual parts of the flower was determined by organoleptic testing after accumulation of floral odour in glass vials for a couple of hours. The parts tested were the calyx, petals, stamens, and pistil together with the floral receptacle and nectaries.

**Colour.** Colour was studied by photographing purple and white flowers in direct sunlight using a Kodak UV-transmitting filter (18A, 300–400 nm) and the following Kodak Wratten gelatine filters: blue 48, 390–500 nm; green 61, 480–610 nm; red 25, >580 nm. Reflectance at the five wavelengths was measured with reference to a grey scale placed next to the flower photographed. To measure colour change 10 inflorescences containing 53 flowers were followed from bud to senescence.

**Nectar.** The nectar volume in 58 flowers was measured on a sunny day at Thorup Strand in 1991. The 58 flowers were born on nine inflorescences, on what was presumed to be nine individual plants. The inflorescences were bagged with fine-meshed nylon

bags for 24 hours before nectar volumes were measured by removing the calyx and petals and placing a 1 µl Vitrex micropipette into one of the access holes. If there was more than 1 µl nectar in the flower several pipettes were used. Variation in nectar volume during two very sunny days (9 and 11 June, 1992) was determined at Thorup Strand by measuring the nectar volumes in flowers that had been bagged the previous evening. Relative humidity was measured on the same days. Nectar from three flowers was lumped to measure nectar concentration, using a hand refractometer (Index Instruments DR 50–80).

**Pollen.** All pollen grains in a single anther from ten randomly chosen flowers were counted under a microscope (all anthers are uniform). Pollen viability was measured as pollen stainability in lactophenol-aniline blue and 500 grains from each of 10 randomly chosen flowers were examined. Fresh pollen from 5 different flowers was examined for content of starch with a JKJ-solution and for content of fat with Sudan IV.

**Breeding system.** The duration of the male and female phase was determined by bagging 29 randomly chosen inflorescences that had all flowers in the early bud stage. Every day the number of pollen grains in one anther was counted and stigma receptivity was tested using the 30% H<sub>2</sub>O<sub>2</sub> test (ZEISLER 1938, GALEN & PLOWRIGHT 1987) in several buds or flowers. Pollen/ovule-ratios for ten flowers were determined by counting the ovules and all pollen grains from one anther in the same flower.

## Pollinators

The behaviour of insects during their visits was observed and individuals of each species visiting the flowers were caught for identification. At Thorup Strand, the bees were observed and caught from 6 June to 6 July, 1991, and from 1 to 20 June, 1992.

## Results

### Plant characters affecting pollination

**Population density.** Populations of *L. japonicus* are generally very dense. In 1991 during the peak flowering period there were up to 400 open flowers per m<sup>2</sup> at Thorup Strand, in 1992 there were about 75 per m<sup>2</sup> in the study plot. Genets have many ramets, due to the long rhizomes, and every ramet has one or more inflorescences with 4 to 10 flowers. The clonal growth and the large floral standards characteristic of *L. japonicus* are likely to attract bees from considerable distances.

**Fragrance.** Like most other *Lathyrus* species, *L. japonicus* has only a faint aromatic smell. The smell stems from the calyx (with glandular hairs), stamens, pistil, nectaries, and floral receptacle; the petals do not smell. *Lathyrus odoratus* and *L. tuberosus* are the only *Lathyrus* species reported having a strong delicate odour (KUPICHA 1983).

**Colour.** The purple flowers reflect red and blue and absorb green and UV light (Fig. 1A–E). The flower has

At Ajstrup Strand, bee behaviour was studied from 12 to 15 July, 1991 and at Nordreisa beach from 30 July to 4 August, 1991.

Observations on flight distance, number of flowers visited per inflorescence, handling time (seconds per flower), and observations to calculate foraging rate (number of flowers visited per minute) were tape recorded.

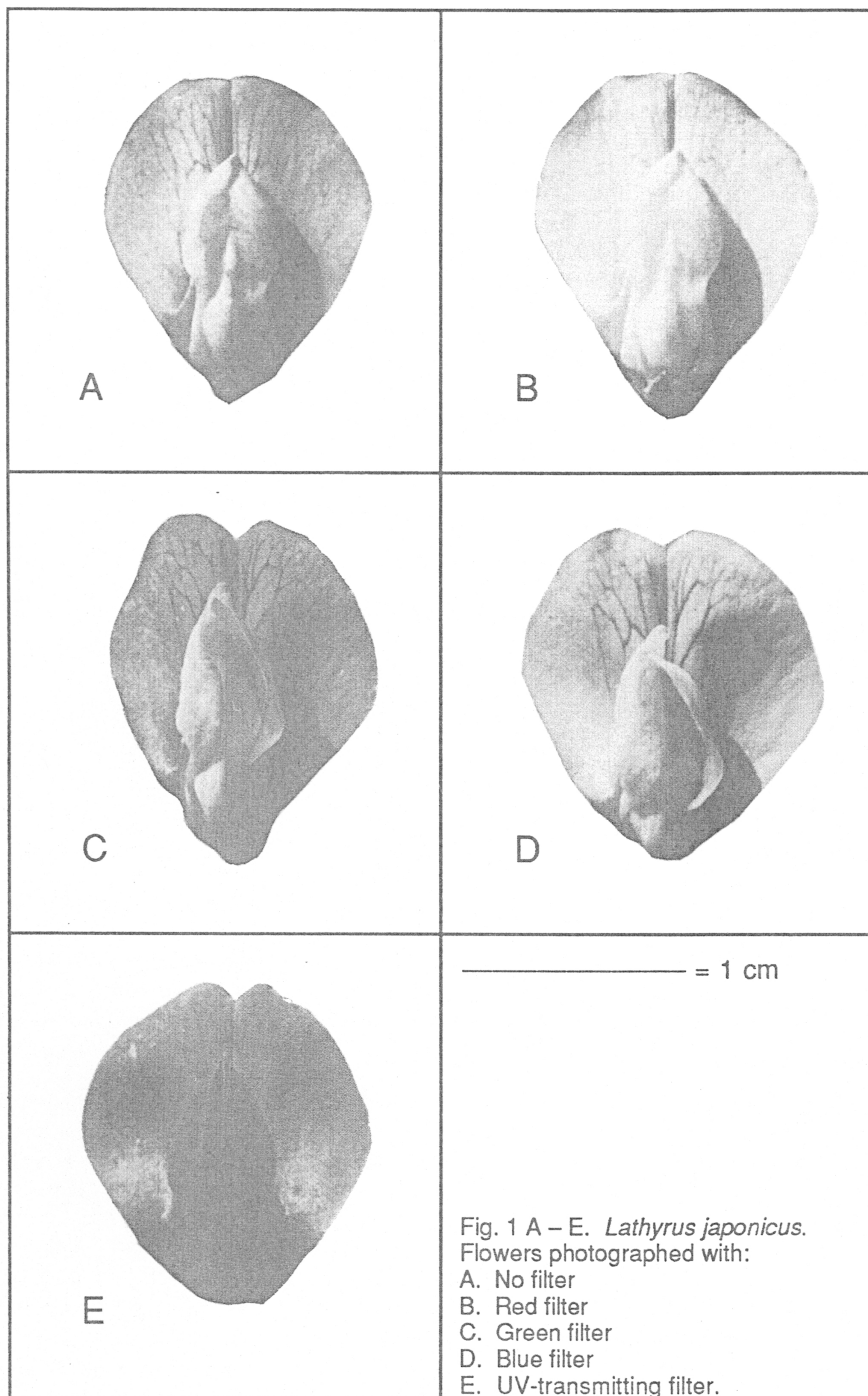
Pollen loads from the pollen baskets of bumblebees (*Bombus* spp.) and from the ventral sides of the abdomen of mason bees (*Osmia* sp.) were investigated. The pollen loads were suspended in water and 1,000 pollen grains from each individual were identified.

Distance to nearest neighbour inflorescence was determined by pretending a bee would start in a flower at inflorescence one and always fly to the nearest flower in another inflorescence, ending after the visit of 100 inflorescences; this procedure was repeated seven times giving a total of 700 measures of inflorescence-to-inflorescence distances.

Variation in bee activity during the day was observed at Thorup Strand from 8 to 12 June, 1992; during this period the weather did not change (temperatures were measured on 9 June, 1992). In a representative 13.5 m<sup>2</sup> study plot all open *L. japonicus* flowers were counted once every day, and the number of open flowers per inflorescence was counted on 424 inflorescences on 12 June, 1992, a day representative of the main flowering period. The number of flowers visited by bumblebees was registered during 30, 25–60 minute periods evenly distributed over the day (7.00–22.00 hours; European Summer Time, i.e., 2 hours ahead of GMT). The total observation time was 16 hours. From this I estimated the average number of flowers visited per two-hour interval. The average number of visits per open flower per day was estimated by dividing the sum of the number of flowers visited per two-hour intervals by the average number of open flowers in the study plot.

nectar guides in the blue spectrum (Fig. 1D) but no UV-pattern, and the change in colour from purple to violet before wilting does not affect reflection patterns. The white flowers reflect red, green, and blue and absorb UV.

**Nectar.** In the dry summer of 1992, the purple and violet phase of the flower lasted one day (purple,  $\bar{x} = 1.2 \pm 0.6$  sd days; violet,  $\bar{x} = 0.8 \pm 0.6$  sd;  $n = 53$ ), whereas in 1991 the flowers lasted longer (purple phase, 5 days; violet phase at least 1 day;  $n = 14$ ). The colour change from purple to violet before wilting was followed by a small non-significant decline in nectar production (Fig. 2). The diurnal variation in nectar present in flowers protected from pollinators and nectar robbers (Fig. 3), indicates that the nectar volume is affected by variation in both evaporation and nectar secretion. Early in the morning nectar volumes were high, presumably because of accumulation of nectar produced since the previous evening (Fig. 3). Increasing evaporation is the most likely explanation for a decline in nectar volumes as temperatures rose and the air became increasingly dryer (Fig. 3). That the



decline did not continue in spite of low humidity may indicate that the plants increased nectar production for a few hours in the early afternoon. Nectar concentration in the morning was 30–32% (3 measurements).

**Pollen.** Stamens produced a mean of  $4,583 \pm 492$  sd pollen grains ( $n = 10$ ), corresponding to 40,000–50,000 grains per flower. Pollen viability was on average  $97.6\% \pm 1.4\%$  sd ( $n = 10$ ). Pollen reacted

positively with Sudan IV and negatively with JKJ, indicating fatty substances and a lack of starch.

**Breeding system.** When the flower opens, the stigma can be receptive as soon as the cuticle of the stigmatic papillae is destroyed, e.g., by a bee. Before this happens viable pollen has been released, placed in the stylar brush, and accumulated in the keel where it covers and surrounds the stigma and style. Thus,

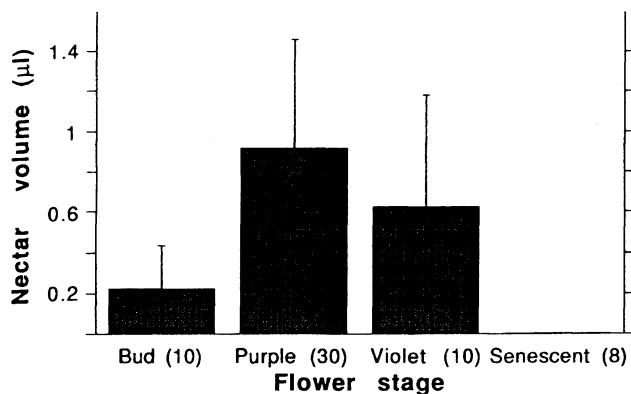


Fig. 2. Nectar volume per flower in successive stages of flower age, Thorup Strand, 18 June, 1991. Standard deviations are given by vertical bars. Sample sizes are given in parentheses at the x-axis.

because viable pollen is present around the potentially receptive stigma *L. japonicus* is functionally homogamous.

The average P/O-ratio was  $6,384 \pm 1,298$  sd ( $n = 10$ ), assigning the flower to xenogamy in CRUDEN'S (1977) classification of P/O-ratios and breeding systems.

### Pollinator guild

At Thorup Strand, *L. japonicus* was pollinated by three species of bumblebees (*Bombus* spp.) and one species of mason bee (*Osmia* sp.; Table 1). Both bumblebees and mason bees sucked nectar and collected pollen, but nectar foraging predominated. The stigma and style with pollen brush touch the bees ventrally on thorax and abdomen, and often also laterally between thorax and abdomen. The mason bees are abdomen collectors, and pure *L. japonicus*

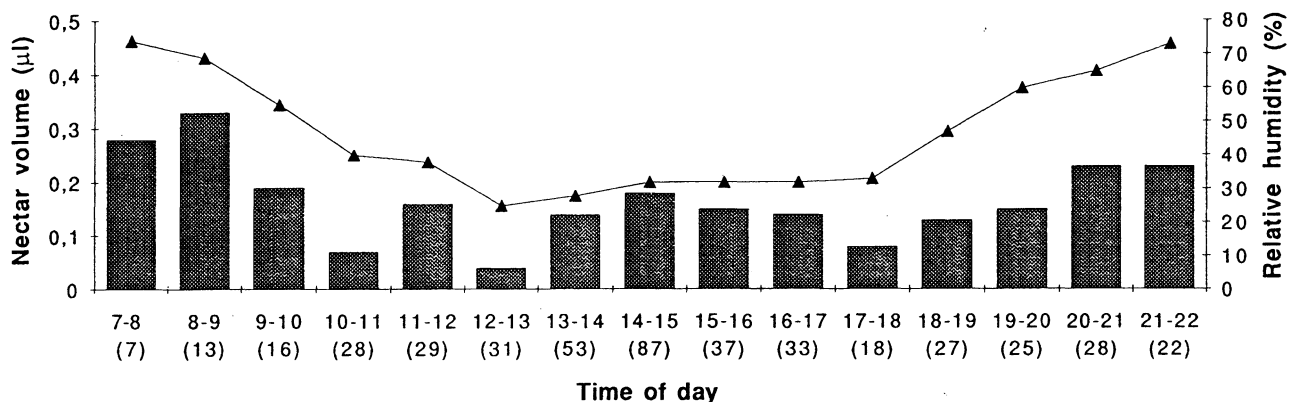


Fig. 3. Average nectar volume per flower (bars) and relative humidity (▲) in one hour periods from 7.00 to 22.00 hour at Thorup Strand, 9 and 11 June, 1992. Sample sizes are given in parentheses.

Table 1. Presence of pollinators and nectar robbers and thieves (w, worker; q, queen) on *Lathyrus japonicus* at Thorup Strand (TS), Ajstrup Strand (AS) both in Denmark, and at Nordreisa beach in northern Norway (N), and whether the species of bumblebee is known to occur in Denmark and northern Norway according to LØKEN (1973).

Species		Pollinator, nectar robber/thief	Locality	Proboscis length*)	Distribution
<i>Bombus lapidarius</i> L.	q	pollinator	TS, AS	$10.85 \pm 0.47$	Denmark
<i>B. lapidarius</i> L.	w	pollinator	TS, AS	$6.96 \pm 0.68$	Denmark
<i>B. pascuorum</i> SCOP.	q	pollinator	TS, AS, N	$10.62 \pm 0.52$	Denmark, N Norway
<i>B. pascuorum</i> SCOP.	w	pollinator	TS, AS, N	$7.89 \pm 0.67$	Denmark, N Norway
<i>B. hortorum</i> L.	q	pollinator	N	$14.60 \pm 0.39$	Denmark, N Norway
<i>B. hortorum</i> L.	w	pollinator	AS, N	$12.42 \pm 0.97$	Denmark, N Norway
<i>B. terrestris</i> L.	q	pollinator, nectar robber/thief	TS, AS	$10.10 \pm 0.41$	Denmark
<i>B. terrestris</i> L.	w	nectar robber/thief	TS, AS	$7.85 \pm 0.57$	Denmark
<i>Osmia</i> sp.		pollinator	TS		
<i>Apis mellifera</i> L.	w	nectar thief	TS	5.9	
<i>Coelioxys</i> sp.		nectar thief	TS		
<i>Aporia crataegi</i> L.		nectar thief	TS		
<i>Clossiana selene</i> DEN. & SCHIFF.		nectar thief	TS		
<i>Lycaena hippothoe</i> L.		nectar thief	TS		

\*) Proboscis length from PEKKARINEN (1979) except for *A. mellifera* which is from STAPEL (1933).

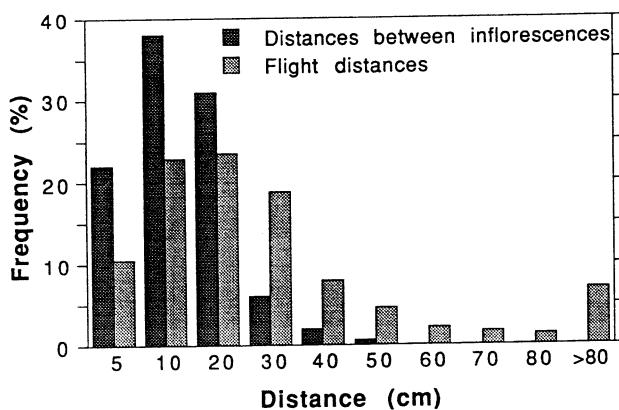


Fig. 4. Frequency distribution of nearest neighbour inflorescences ( $n = 700$ ) and of flight distances for *B. pascuorum* ( $n = 759$  flight distances; 21 individuals), Thorup Strand, June, 1992. The group '> 80' cm includes 52 long-distance-flights of more than 30 m.

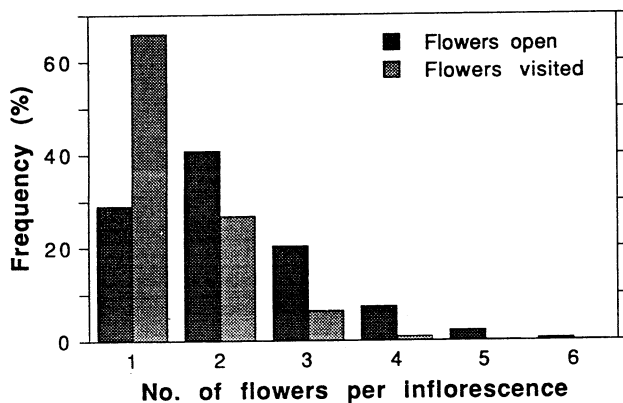


Fig. 5. Frequency distribution of number of open flowers on individual inflorescences ( $n = 424$  inflorescences) and of flowers visited per inflorescence by workers and queens of *B. pascuorum* ( $n = 1,195$  inflorescence visits; 34 individuals), Thorup Strand, June, 1992.

pollen was found on *Osmia* sp. ( $n = 5$ ). At Thorup Strand there was a high proportion of *L. japonicus* pollen in the pollen baskets of *B. lapidarius* and *B. pascuorum* ranging from 96% to 100% ( $\bar{x} = 98.9\%$ ,  $n = 4$ ;  $\bar{x} = 99.2\%$ ,  $n = 9$ , respectively) and only one of five individuals of *B. terrestris* had other pollen than *L. japonicus* ( $\bar{x} = 94.4\%$ ,  $n = 5$ ). At Ajstrup Strand, *B. pascuorum* and *B. terrestris* were less inclined to collect pure *L. japonicus* pollen:  $\bar{x} = 80.5\%$  (range 9.5–100%,  $n = 9$ ); and  $\bar{x} = 33.0\%$  (range 0–99.1%,  $n = 3$ ), respectively. The average for *B. pascuorum* at Nordreisa beach was 90.9% (range 38.5–100%,  $n = 7$ ). At the studied localities few other species were flowering simultaneously with *L. japonicus*, and most non-*Lathyrus* pollen found on the

bees at Ajstrup Strand came from *Rosa rugosa* which was growing next to the dense *L. japonicus* population.

Workers of *B. terrestris* were observed both as primary nectar robbers (sensu INOUE 1980), biting holes in the flowers, and as secondary robbers, using holes already made. *Apis mellifera* acted as a secondary nectar robber or it was a nectar thief gaining direct access to the nectar from the side of the flowers without touching the anthers. Three species of butterflies also sucked nectar from the side (Table 1).

### Bee activity and flight patterns

The frequency distribution of inflorescence-to-inflorescence distances was leptocurtic (Fig. 4;  $\bar{x} = 14.2 \pm 8.9$  sd, skewness ( $g_1$ ) = 1.6, kurtosis ( $g_2$ ) = 5.3) and so was the frequency distribution of the distances *B. pascuorum* covered when flying from inflorescence to inflorescence (Fig. 4;  $\bar{x} = 23.8 \pm 16.6$  sd, skewness ( $g_1$ ) = 1.2, kurtosis ( $g_2$ ) = 1.4). The two distributions differed significantly (Kolmogorov-Smirnov;  $D = 0.299$ ,  $p < 0.001$ , SOKAL & ROHLF 1981). The bees flew longer than necessary which may indicate that the cost of flying in *B. pascuorum* was of minor importance. After leaving a patch, the bumblebees flew parallel to the dunes when they moved to neighbouring patches of *L. japonicus* or to patches much further away.

Table 2. Handling time (seconds per flower) and foraging rate (flower visits per minute) of two species of bumblebees at two localities in Denmark;  $n$  is total number of visits, number of bumblebees in parentheses, and min is number of minutes with observations.

Locality Species	Handling time			Foraging rate	
	$\bar{x}$	sd	n	flowers/min	min
Thorup Strand					
<i>B. lapidarius</i>	4.3	3.2	144 (3)	6.0	23
<i>B. pascuorum</i>	1.7	1.2	983 (20)	13.3	128
Ajstrup Strand					
<i>B. pascuorum</i>	1.7	1.4	1631 (77)	14.6	112

In the main flowering season in 1992, 71% of the inflorescences had at least 2 open flowers, but only 34% of all visits of *B. pascuorum* were to more than one flower per inflorescence (Fig. 5). The two distributions differ significantly (Kolmogorov-Smirnov;  $D = 0.369$ ,  $p < 0.001$ ). *Bombus lapidarius* behaved in a manner similar to *B. pascuorum*. Handling time of the first flower visited by *B. pascuorum* in an inflorescence was independent of the number of flowers visited per inflorescence (Kolmogorov-Smirnov;  $D = 0.048$ ,  $n_1 = 470$ ,  $n_2 = 230$ ,  $p > 0.50$ ; frequency distribution of handling times when one flower in an

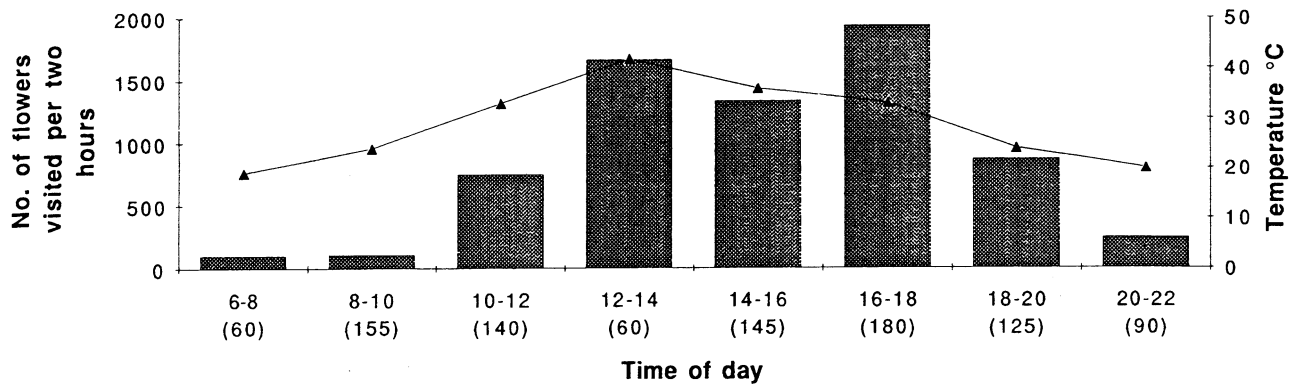


Fig. 6. Estimated number of flowers visited by bumblebees per two-hour interval in a 13.5 m<sup>2</sup> plot (bars) and variation in temperature 10 cm above the ground (▲), Thorup Strand 8 to 11 June, 1992. Total observation minutes for the intervals are given in parentheses.

inflorescence was visited vs. when two or more flowers were visited; handling time was measured to the nearest half second).

*Bombus lapidarius* had longer handling times and visited fewer flowers per minute than *B. pascuorum* (Table 2), and in *B. pascuorum* there were no differences in handling time and foraging rate among the two localities.

## Discussion

### Plant characters affecting pollination

The evolution of UV-pattern does not seem to be correlated with the taxonomic sections currently recognized in *Lathyrus* since species of the same section may have different UV-patterns (KAY 1987, ROSEN & BARTHOLOTT 1991), while those of different sections may show the same pattern as, for example, *L. japonicus* from sect. *Orobis* (this study) and *L. aphaca* from sect. *Aphaca* (KAY 1987). Photos of more species might give a better differentiation and reveal trends within the genus. Sympatric species of *Lathyrus* should be compared because they might have evolved different UV-patterns in order to be recognized by pollinators. Majoring (visiting more frequently) by pollinators on specific *Lathyrus* species would help avoid stigma clogging and allow more efficient resource use in the face of intra- and interspecific plant competition.

Colour change from purple to violet as observed in *L. japonicus* has been reported from several other species of *Lathyrus* belonging to different sections, e.g., *L. vernus*, *L. linifolius* (both sect. *Orobis*), *L. sylvestris*, and *L. latifolius* (both sect. *Lathyrus*). In *L. japonicus* the change in colour is not likely to give the bees any information about nectar volume because nectar volumes were nearly equal in purple and violet flowers (Fig. 2). As expected from this the bees visited purple as well as violet flowers. WEISS (1991) gives a survey of colour-changing flowers in which pollinators respond to the colour change;

A few bumblebees visited flowers early in the morning but as the temperature rose bee numbers increased, and bumblebee activity was high during the entire afternoon (Fig. 6). It only declined as the temperature dropped in the evening (Fig. 6).

On sunny days without rain each flower was visited by bumblebees on average 7 times per day.

none of these cases involve a change from purple to violet, but violet and blue flowers of *Anchusa strigosa* contain different nectar volumes (KADMON et al. 1991).

The pollen/ovule-ratio found in *L. japonicus*, 6,384, was about twice as high as in the four other species of *Lathyrus* that have been investigated: about 3,250 in *L. latifolius* (VALERO et al. 1986a: Fig. 2), about 2,000 in *L. sylvestris* (VALERO et al. 1986a: Fig. 2), on average  $3,269 \pm 97$  sd ( $n = 4$ ) in *L. linifolius* (ASMUSSEN unpubl.), and on average  $2,909 \pm 287$  sd ( $n = 6$ ) for *L. pratensis* (ASMUSSEN unpubl.). These five species are perennials and based on their P/O-ratios they are predicted to be facultatively or obligatorily xenogamous according to CRUDEN'S (1977) scheme. Outcrossing in the perennial *Lathyrus* flowers investigated so far (*L. sylvestris*, *L. tuberosus*, and *L. latifolius*) is enforced by the floral tripping mechanism, by which the stigma becomes receptive only after the rupture of the cuticle of the stigma papillae; and then pollen, either self or foreign, can germinate. Investigations on the breeding system of *L. japonicus* are presently being carried out to determine the selfing rate.

### Pollinator guild

Many other species of *Lathyrus* have a pollinator guild similar to the one found in *L. japonicus*, that is, several species of bumblebees and one to several species of solitary

Table 3. Pollinators in five sections of *Lathyrus* (sectional classification following KUPICHA 1983). Butterflies are unlikely to be pollinators of *Lathyrus* and are therefore omitted.

Section	Species	Pollinator guild	Source	
<i>Lathyrostylis</i>	<i>L. brachypterus</i>	<i>Bombus</i> spp. (Apidae) <i>Megachile</i> spp. (Megachilidae)	KNUTH 1898	
<i>Lasthyrus</i>	<i>L. cirrhosus</i>	<i>Bombus</i> spp. (Apidae)	KNUTH 1898	
	<i>L. grandiflorus</i>	<i>Eucera longicornis</i> (Anthophoridae) <i>Megachile fasciata</i> (Megachilidae) <i>Xylocopa violacea</i> (Anthophoridae)	KNUTH 1898, TEPPNER 1988	
	<i>L. heterophyllus</i>	<i>Bombus</i> spp. (Apidae) <i>Eucera</i> spp. (Anthophoridae) <i>Megachile</i> spp. (Megachilidae) <i>Xylocopa violacea</i> (Anthophoridae)	KNUTH 1898, GAMS 1924	
	<i>L. hirsutus</i>	<i>Bombus pascuorum</i> (Apidae) <i>Megachile fasciata</i> (Megachilidae)	KNUTH 1898	
	<i>L. latifolius</i>	<i>Bombus</i> spp. (Apidae) <i>Eucera longicornis</i> (Anthophoridae) <i>Megachile</i> spp. (Megachilidae) <i>Osmia tridentata</i> (Megachilidae) <i>Xylocopa violacea</i> (Anthophoridae)	KNUTH 1898, WESTERKAMP 1987, WESTRICH 1989	
	<i>L. odoratus</i>	<i>Anthidium manicatum</i> (Megachilidae) <i>Apis mellifera</i> (Apidae) <i>Megachile willughbiella</i> (Megachilidae)	DARWIN 1876, KNUTH 1898	
	<i>L. rotundifolius</i>	<i>Bombus pascuorum</i> (Apidae) <i>Megachile fasciata</i> (Megachilidae)	KNUTH 1898	
	<i>L. sativus</i>	<i>Apis cerana</i> (Apidae) <i>Apis mellifera</i> (Apidae)	KNUTH 1898, CRANE & WALKER 1984	
	<i>L. sylvestris</i>	<i>Anthophora</i> sp. (Anthophoridae) <i>Bombus</i> spp. (Apidae) <i>Eucera longicornis</i> (Anthophoridae) <i>Megachile</i> spp. (Megachilidae) <i>Melitturga clavicornis</i> (Andrenidae) <i>Osmia</i> spp. (Megachilidae) <i>Trachusa</i> spp. (Megachilidae) <i>Xylocopa violacea</i> (Anthophoridae)	MÜLLER 1873, KNUTH 1898, WESTERKAMP 1987, WESTRICH 1989	
		<i>L. tingitanus</i>	<i>Bombus pascuorum</i> (Apidae)	WESTERKAMP 1987
		<i>L. tuberosus</i>	<i>Megachile</i> spp. (Megachilidae) <i>Halictus sexcinctus</i> (Halictidae)	KNUTH 1898, TEPPNER 1988
	<i>Linearicarpus</i> <i>Orobus</i>	<i>L. sphaericus</i>	<i>Osmia</i> sp. (Megachilidae)	ASMUSSEN unpubl. obs.
		<i>L. aureus</i>	<i>Bombus</i> spp. (Apidae)	KNUTH 1898
		<i>L. incurvus</i>	<i>Bombus pascuorum</i> (Apidae)	KNUTH 1898
<i>L. japonicus</i>		<i>Bombus</i> spp. (Apidae) <i>Osmia</i> sp. (Megachilidae)	KNUTH 1898, GAMS 1924, this study	
<i>L. laevigatus</i>		<i>Lasioglossum punctatissimum</i> (Halictidae)	WESTERKAMP 1987	
<i>L. linifolius</i>		<i>Andrena</i> spp. (Andrenidae) <i>Anthophora pilipes</i> (Anthophoridae) <i>Bombus</i> spp. (Apidae) <i>Eucera longicornis</i> (Anthophoridae) <i>Halictus</i> spp. (Halictidae) <i>Megachile circumcincta</i> (Megachilidae) <i>Osmia pilicornis</i> (Megachilidae)	MÜLLER 1873, KNUTH 1898, WILLIS & BURKILL 1903, KRATOCHWIL 1988, WESTRICH 1989	
		<i>L. niger</i>	<i>Bombus</i> spp. (Apidae) <i>Osmia rufa</i> (Megachilidae)	KNUTH 1898, GAMS 1924, WESTERKAMP 1987
		<i>L. occidentalis</i>	<i>Bombus</i> sp. (Apidae)	KNUTH 1898
		<i>L. palustris</i>	<i>Bombus</i> spp. (Apidae)	KNUTH 1898, WESTERKAMP 1987
		<i>L. splendens</i> <i>L. venetus</i>	Hummingbird <i>Bombus hortorum</i> (Apidae) <i>Megachile ericetorum</i> (Megachilidae) <i>Osmia rufa</i> (Megachilidae) <i>Xylocopa violacea</i> (Anthophoridae)	ARROYO 1981 KNUTH 1898
	<i>L. vernus</i>	<i>Andrena lathyri</i> (Andrenidae) <i>Bombus</i> spp. (Apidae) <i>Osmia</i> spp. (Megachilidae)	MÜLLER 1873, KNUTH 1898, GAMS 1924, WESTERKAMP 1987, KRATOCHWIL 1988, WESTRICH 1989	
<i>Pratensis</i>	<i>L. pratensis</i>	<i>Andrena lathyri</i> (Andrenidae) <i>Bombus</i> spp. (Apidae) <i>Eucera</i> spp. (Anthophoridae) <i>Megachile</i> spp. (Megachilidae) <i>Osmia</i> spp. (Megachilidae) <i>Trachusa byssina</i> (Megachilidae) <i>Xylocopa violacea</i> (Anthophoridae)	MÜLLER 1873, KNUTH 1898, WILLIS & BURKILL 1903, WESTERKAMP 1987, WESTRICH 1989	



bees (e.g., *Andrena*, *Eucera*, *Megachile*, *Osmia*; Table 3). Such broad pollinator guilds are common for pioneers and for plants growing in open, disturbed, or unpredictable habitats like most species of *Lathyrus*, including *L. japonicus*. Nevertheless there are exceptions. For example the very specialised relationships between *L. grandiflorus* and *Xylocopa violacea* (TEPPNER 1988); *L. splendens* and hummingbirds (ARROYO 1981); and some of the small-flowered species like *L. sphaericus* and small megachilids (ASMUSSEN pers. obs.).

*Lathyrus japonicus* flowers were larger at the study site in northern Norway than in Denmark (ASMUSSEN in prep.), but this is not due to differences in the pollinator guilds at the two sites, which largely consisted of the same species. One would have expected the larger-flowered subspecies to be pollinated by larger bees or bees with longer proboscises, but at least in *B. pascuorum*, which is a common pollinator of *L. japonicus* in both countries, there does not seem to exist a cline in body size or tongue length towards the north (LØKEN 1973). The next hypothesis to test would be whether there is a difference between the *Lathyrus* populations in Denmark and in northern Norway in the relative frequency of visits by short-tongued and long-tongued bees. An indication of such a difference may be that the longer-tongued *B. hortorum* was observed very few times in Denmark and at one locality only, whereas in northern Norway it frequently sucked nectar from *L. japonicus*.

### Nectar, bee activity, and bee flight patterns

At all times of the day many flowers contained no nectar or only small volumes of nectar, and this may explain why *B. pascuorum* rarely chose the nearest inflorescence when flying from inflorescence to inflorescence. Also other studies have found that bees fly more in one direction and fly longer distances when nectar volumes are small, than when nectar volumes are high (PYKE 1978; HEINRICH 1979; WADDINGTON 1980).

The fact that the bees visited just one flower per inflorescence more often than inferred from the number of open flowers per inflorescence could have one of the following explanations. The bees might be testing the first flower and stay if nectar is present, else leave. My data on handling time of the first flower visited in an inflorescence do not support this hypothesis, but this might be due to too coarse a graduation of handling time because an 0.5 second handling time may include both testing and nectar sucking. For example in *Chilopsis* flowers (*Bignoniaceae*) it takes bumblebees only 0.5 seconds to suck 0.15 to 1 µl nectar

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(HEINRICH 1983); these nectar volumes are within the range of what is common in *L. japonicus* flowers. Another explanation could be that because of the dense populations of *L. japonicus* the bees did not experience the flowers as grouped in inflorescences, and because of the short distances between the inflorescences, differences in the cost of flights between visiting another flower in the same inflorescence and one in another inflorescence might be minor. A third explanation could have to do with resource distribution. If flowers containing nectar are distributed at random, the bees should fly to the nearest flower because the probability that it will contain nectar is the same as for a flower further away. If the nectar containing flowers are patchily distributed, the bees should fly to the nearest neighbour when in a 'rich' patch and further away when in a 'poor' patch (WADDINGTON 1980).

The observed flight pattern and especially the long distance flights are likely to be advantageous for the flower in terms of outcrossing. Thus, although population structure of *L. japonicus* is clonal, there is genetic variability over short distances; e.g., within a patch some individuals have purple and others have white flowers, some plants are glabrous and some are pubescent, and leaf morphology is also highly variable (pers. obs.). This is consistent with what is found for *L. latifolius* (GODT & HAMRICK 1993), i.e., a leptocurtic pattern of gene movement via pollen, including several long distance movements, and outcrossing rates between 0.87 and 0.90.

In spite of the harsh environment in which *L. japonicus* grows, the number of bumblebees does not seem to limit the number of flowers pollinated. In fact the chance for more than one visit per flower was high due to the high number of active bees and their short visits to the flowers. Although rain reduces the probability of a flower being pollinated in terms of bee activity, rain may also have a positive effect because during periods of high precipitation (1991) flower life time is more than twice as long as during dry periods (1992).

In summary, *L. japonicus* flowers are functionally homogamous and the duration of anthesis differed between years according to weather. Nectar volumes were high enough to ensure that pollinators visited *L. japonicus* flowers (cf. HEINRICH 1979). Pollinator guilds at the three localities in Denmark and Norway and on the two subspecies were largely similar, and *B. pascuorum* was the most important pollinator because it was the most abundant, visited most flowers per second, and exhibited high floral constancy, possibly due to a lack of alternatives. The behaviour of the bees, together with morphology and physiology of the flower, promotes outcrossing.

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## Buchbesprechung

MOBERG, R., und HOLMÅSEN, I.: **Flechten von Nord- und Mitteleuropa – Ein Bestimmungsbuch**. Übersetzt von UTE JÜLICH. – Stuttgart; Jena; New York: G. Fischer, 1992. – 237 S., 350 Abb. (überwiegend Farbfotos), 300 Verbreitungskarten. Glanzkarton, DM 78,–. ISBN 3-437-20471-8.

Vorliegendes Buch stellt eine Übersetzung der vor genau 10 Jahren erschienenen schwedischen Originalausgabe dar. Damals war das Werk als eines der ersten reich bebilderten Flechtenbestimmungsbücher als wegweisend zu bezeichnen. Die jetzt vorliegende Übersetzung weist jedoch zahlreiche Mängel auf, die bei einer gründlicheren Überarbeitung vermeidbar gewesen wären.

In einleitenden Kapiteln wird der Leser über Bau, Vermehrung, Wachstum, Ökologie und Verbreitung, Chemie und praktische Verwendung von Flechten informiert. Auch das Sammeln und Aufbewahren von Flechten wird ausführlich beschrieben. Es folgen Gattungsbeschreibungen und Bestimmungsschlüssel der aufgeführten Strauch- und Blattflechten. Der Bestimmungsschlüssel der Flechtengattungen jedoch folgt davon losgelöst erst nach dem Hauptteil. Bereits in den einleitenden Kapiteln haben sich einige Fehler eingeschlichen, die zumindest teilweise auch einer fehlerhaften Übersetzung anzulasten sind. Im Kapitel „Bau der Flechten“ werden auch Rotalgen als selten vorkommende Algenpartner erwähnt. Hier dürfte eine Verwechslung mit den