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POLLINATION BY A GUILD OF FLUCTUATING MOTH POPULATIONS: OPTION FOR UNSPECIALIZATION IN *SILENE VULGARIS*

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SUMMARY

(1) The pollinating efficiency of moths was examined during four seasons by counting the number of pollen grains that individual moths deposited on the stigmas of virgin female flowers of *Silene vulgaris*.

(2) Experimental pollination showed that c. 150 pollen grains per flower were required to achieve the average natural full seed-set in the plant population. Although 57% of the flower-visiting moths deposited pollen, only about 10% of the moth visits delivered ≥ 150 pollen grains in one visit to virgin female flowers, indicating that seed-set usually originated from multiple pollinator visits.

(3) Pollen receipt indicated pollination by a guild of noctuid and sphingid moths. The abundance of the dominating pollinator species varied strongly between years.

(4) Most species deposited about the same mean number of pollen grains, although they were taxonomically diverse and had different flower-visiting behaviours and proboscis lengths. Even noctuid moths of the genus *Hadena*, known as associated larval seed predators of *S. vulgaris*, were not especially frequent or efficient pollinators despite the fact that these moths influence their larval food resource through pollination.

(5) The annual and seasonal variation in abundance among pollinator species and lack of variation in pollination efficiency among them are factors which counteract specializational trends and control evolutionary retention of plastic and unspecialized floral traits in *S. vulgaris*. They thereby provide an option for opportunistic responses in this species.

INTRODUCTION

Insect flower visitors have often been uncritically reported as ‘pollinators’ of the plants visited. However, conclusions from quantitative estimates of differential visitation frequencies as a measure of efficiency can be blurred by the fact that many visitors may act solely as nectar thieves, although greatly outnumbering the ‘legitimate’ pollinator species (Haber & Frankie 1982). Information on the number of pollen grains carried by flower visitors can provide essential information about the relative importance of different pollinator species in many systems, but pollen may fall off during the capture of such visitors for study, and some species seldom act as pollinators although they readily get contaminated with pollen (Janzen 1977; Harder *et al.* 1985). The combination of abundance and efficiency has to be taken into account in judging the relative importance of different flower-visiting insect species as pollinators (Spears 1983; Young 1988 and references therein; Herrera 1989).

In recent years, some workers have presented data on the number of pollen grains actually deposited on stigmas (Levin & Berube 1972; Primack & Silander 1975; Thomson & Plowright 1980; Tepedino 1981; Bertin 1982; Morse & Fritz 1983; Motten 1983; Schemske & Horovitz 1984; Harder *et al.* 1985; Sugden 1986; Thomson 1986; Herrera 1987; Yeboah Gyan & Woodell 1987). In addition, components of plant fitness in relation to visitors have been studied by analysing the seed-set resulting from a single insect visit (Motten *et al.* 1981; Tepedino 1981; Parker 1981, 1982; Spears 1983; Young 1988).

For a plant to specialize, it seems necessary that visitor species differ in their interactions with the plant. An increase in the number of visits by efficient pollinators may increase the reproductive success of individual plants. For example, tongue length is often related to the efficiency of pollinators (Miller 1981; Nilsson 1988; Herrera 1989). If plant fitness is low due to strongly skewed morphological interactions with long-tongued pollinators, plants with longer corollas or spurs will be favoured. If, however, skewness is small or absent due to interactions being diverse and effects diffuse, plants are predicted to exhibit floral unspecialization, i.e. to evolve traits allowing a large cadre of pollinators. The basic purpose of this study was to examine the actual diversity of pollinator efficiencies in such a relatively unspecialized moth-driven system.

The present study is the first attempt to investigate pollinator efficiency in a moth-pollinated plant, *Silene vulgaris* (Moench) Garcke (Caryophyllaceae). The purposes were (i) to determine the absolute as well as the relative ability of different pollinators (including those moths that also act as larval seed predators) to deposit pollen on stigmas, (ii) to examine how morphological and behavioural traits affect pollen deposition, and (iii) to relate the number of pollen grains deposited on stigmas to the number of seeds produced by the plant. By this approach, the effects of pollinators on components of the plant's fitness could be explored.

THE SPECIES AND THE SYSTEM

Silene vulgaris is a deep-rooted perennial distributed throughout Europe (Marsden-Jones & Turrill 1957) and it has spread to North America (Maw 1976). It occurs in a variety of life-forms (Raunkiaer 1934; Aeschimann & Bocquet 1980), and grows in a great diversity of habitats, although preferring disturbed areas including roadsides and cultivated ground (Marsden-Jones & Turrill 1957). The plant can be gynodioecious or gynodioecious and has white protandrous flowers with five free petals, the lobes of which spread at right angles at the calyx mouth. The corolla is c. 10 mm deep and surrounded by a strongly inflated calyx. Stamens (5 + 5) and styles (3) protrude from the corolla where they contact visiting insects (Fig. 1). The stamens dehisce at about 20.00 hours, and usually little pollen remains the next morning (personal observation). According to Dulberger & Horovitz (1984), nectar is secreted only at night from the glandular tissue at the base of the stamens.

A large number of insect species are known to visit the flowers of *S. vulgaris*, including bees, flies and moths (Knuth 1898; Marsden-Jones & Turrill 1957). Bees are occasionally seen to extract remaining nectar from the flowers during day-time, mostly when no or very little pollen remains (personal observation). Moths start to visit the flowers at about 22.00 hours at light-intensities around 20 lux, and visitation peaks about 1 h later (personal observation). Various floral traits clearly indicate that

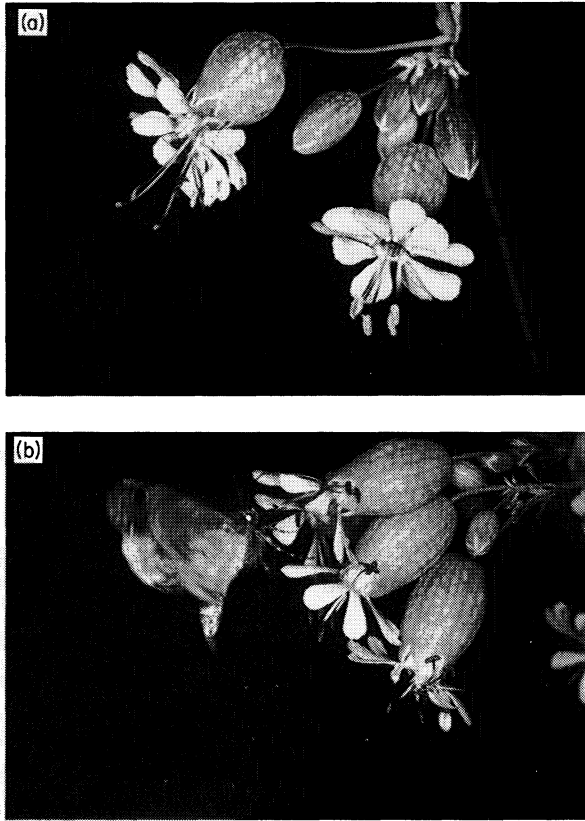


FIG. 1. (a) Hermaphrodite *Silene vulgaris* flowers in female and male phase, respectively. (b) A flower-visiting female of the noctuid *Hadena rivularis* drinking nectar prior to laying an egg in the flower.

S. vulgaris is evolutionarily associated with pollination by moths (Marsden-Jones & Turrill 1957), but nothing has so far been reported about the actual pollination efficiency of the moths involved. Among the various moths reported as visitors, noctuid moths of the genus *Hadena* act as pollinators and also feed as larvae on various Caryophyllaceae plants, then acting as 'parasitic pollinators' (Wahlgren 1924). Eggs are laid singly near the ovary, with oviposition usually preceded by drinking from the flower, which becomes pollinated in the process (Brantjes 1976). In *S. vulgaris*, eggs are laid in flowers by *Hadena confusa*, *H. rivularis* and *H. bicruris*, and on flower buds by *H. perplexa* (Pettersson 1991). According to Brantjes (1976), a brood of *Hadena* larvae will consume more seed capsules than one pair of moths will generate through pollination during their life-time, but he gave no actual data on pollen transfer.

METHODS

The field work was conducted in June and July in 1986 to 1989 near Skogsby on the Baltic island of Öland off the south-eastern coast of Sweden (56°30' N, 16°30' E).

The relationship between pollen deposition and seed-set was studied by experimental pollination. In 1987, twenty series of 5, 10, 20, 40, 80, 150, 300 and 600 pollen grains from randomly chosen *S. vulgaris* individuals were applied to stigmas on flowers of four female plants that had opened in cages. The flower stalks were gently bent and pollen grains applied under a stereo-microscope using a brush. Ovule numbers in flowers from the four experimental plants had the following means: 164.5 ± 12.4 ($n = 16$), 155.8 ± 12.4 ($n = 20$), 162.5 ± 21.6 ($n = 21$) and 155.9 ± 18.6 ($n = 19$); these did not differ significantly, nor did they differ from other plants in the surrounding population; 163.8 ± 16.7 ovules for flowers on hermaphrodite plants ($n = 19$) and 167.4 ± 24.5 for flowers on female plants ($n = 17$) (ANOVA, $F = 1.26$, $P = 0.28$). The seed capsules were later harvested and the number of seeds fertilized by the different pollen loads counted and compared with the number of seeds in capsules from plants in the surrounding population that were collected on the same occasion. In order to compare the number of seeds in capsules of the different sex morphs, naturally pollinated hermaphroditic and female individuals were sampled in 1986.

Within a patch of *S. vulgaris* a 1-m^3 cage of fine nylon-mesh screen was placed over one or two female individuals before flowering to exclude pollinators and thus obtain virgin experimental flowers. Between 22.00 and 24.00 hours (GMT + 2 h) on most nights during the flowering period the cage was removed, and visiting moths were watched while foraging on one to three flowers and then caught. After 23.30 hours an electric lamp with red light was sometimes used to facilitate the moth-catching and other procedures. The moths were killed immediately after capture and stored individually in glass tubes for later determination, measurement of proboscis length and counting of pollen load. The flowers visited were then harvested in sequence and placed singly in plastic tubes with the same code number as the moth tube, for later measurement of the length of corolla and styles, and examination of the styles for pollen. Time and light intensity when each moth arrived, the time it spent at the flower, and its foraging behaviour were recorded.

In order to study the relationship between pollen deposition and the functional distance between the nectaries and the floral sexual organs, flowers were measured. Additional data from flowers on individuals other than the target plant were gathered by collecting one flower from each of twenty females and also one male-phase and one female-phase flower from each of twenty hermaphrodite plants. Flowers were measured for corolla depth (from the base of the petal stalk to the ligula) and distance between the base of the petal stalks and the tip of the stamens or styles.

Data analysis

Because flower-visiting moths often appeared in low numbers, only a limited number could be collected from the target plants each year, and the data for 1986–89 therefore had to be pooled for analysis. Three measures were used to compare the pollination efficiency of the moth species: (i) the percentage of visits during which pollen grains were deposited, (ii) the percentage of visits that resulted in ≥ 150 pollen grains being deposited, and (iii) the mean number of pollen grains that were deposited (blanks omitted). In calculations of mean number of deposited pollen grains, the first visited flower was always used irrespective of how many flowers on the target plant were subsequently visited. The total number of pollen grains deposited by a species over the 4 years was used to calculate its relative importance as

pollinator. Often, more pollen grains than the maximal number that could be used by the plant to produce seeds were deposited on stigmas, and therefore the median score in pollen deposition was used when comparing pollen deposition by moths with the natural seed set in the surrounding population.

Statistical analyses were made using the SAS package (SAS Institute Inc. 1985). Standard deviation was used as a measure of the variability, and Spearman rank correlations were used for testing associations between variables.

RESULTS

Pollen-deposition—seed-set relationship

Seed production is an asymptotic function of pollen deposition, saturating at about 150 pollen grains (Fig. 2), and giving a mean (± 1 S.D.) full seed-set of 58.2 ± 18.1 seeds capsule⁻¹ ($n = 56$). The mean number of seeds in capsules from flowers on plants in the area, naturally pollinated during the same time, was 55.2 ± 11.9 ($n = 21$), and did not differ from the former category (t -test, $P = 0.48$). The mean number of seeds capsule⁻¹ in the previous year was 43.8 ± 15.0 ($n = 32$) in female individuals and 44.5 ± 10.2 ($n = 23$) in hermaphrodite individuals, with no statistical difference between the two sex types (t -test, $P = 0.8$).

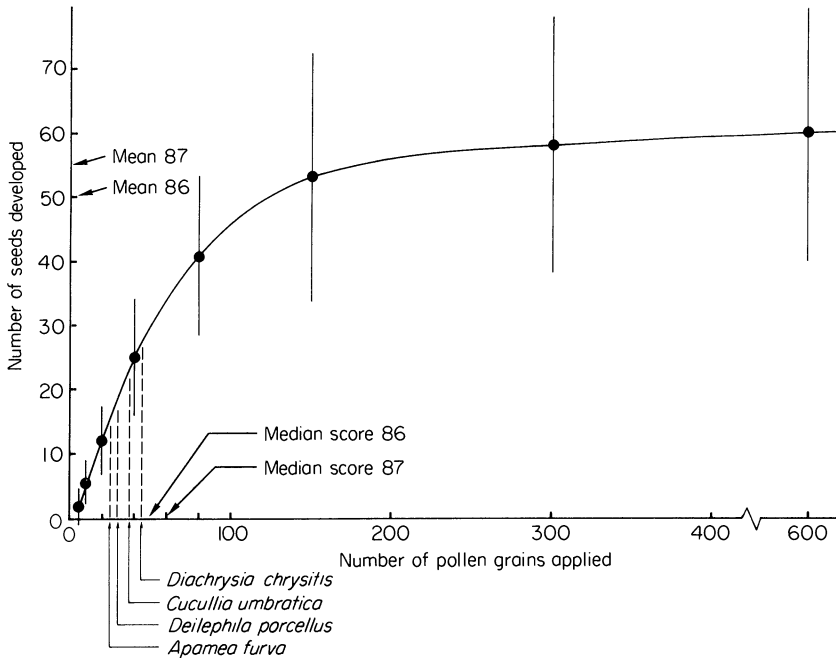


FIG. 2. The relation between the number of experimental pollen grains applied to virgin stigmas and the mean (± 1 S.D.) number of seeds developed in ovaries of female *Silene vulgaris*. The median score in pollen deposition per flower-visit by the most common moth species and their estimated 'one-visit' contribution to seed-set in *S. vulgaris* are included.

Moths as pollinators

During the four seasons, data were collected from 291 individuals representing twenty-four species of noctuid moths and two species of sphingid moths visiting the target *S. vulgaris* flowers. All species that were frequent flower visitors varied greatly in abundance between years (Table 1). For example, most *Cucullia umbratica* and *Autographa gamma* individuals were obtained in a single year and *Apamea furva*, a common visitor during 1986–88, was almost absent in 1989. As a result, also proboscis length of the moths varied significantly between years (ANOVA, $F = 23.4$, $P < 0.001$).

A total of 167 (57%) of the moths delivered pollen grains to stigmas, the distribution being leptocurtic (Fig. 3). There were no differences between years or between the nine most-frequent visitors in the proportions of visits resulting in pollen being deposited (Table 1; $\chi^2_3 = 1.85$, $P = 0.6$ and $\chi^2_8 = 7.3$, $P = 0.5$, respectively).

There was a positive overall correlation between the residual pollen loads on the bodies of moths and the number of pollen grains that had been deposited prior to capture (Fig. 4; $r = 0.56$, $n = 183$, $P < 0.001$). Also, for each of the four most common visitor species, *Apamea furva*, *Diachrysia chrysitis*, *Cucullia umbratica* and *Autographa gamma*, correlations were positive in this respect ($r = 0.66$, $n = 31$, $P < 0.001$; $r = 0.60$, $n = 37$, $P < 0.001$; $r = 0.53$, $n = 22$, $P < 0.05$ and $r = 0.52$, $n = 19$, $P < 0.05$, respectively). However, in twenty-three (14%) of the total number of moths that deposited pollen, a large number of pollen grains (20–250) was found on stigmas although no or very few (< 5) pollen grains remained on the visitor's body. Visits with no pollen deposition were associated with a lack of residual pollen load in 90% of the 136 visitors, but thirteen moths (10%) with moderate to high residual pollen load (20–1000 pollen grains) failed to deposit any pollen at all.

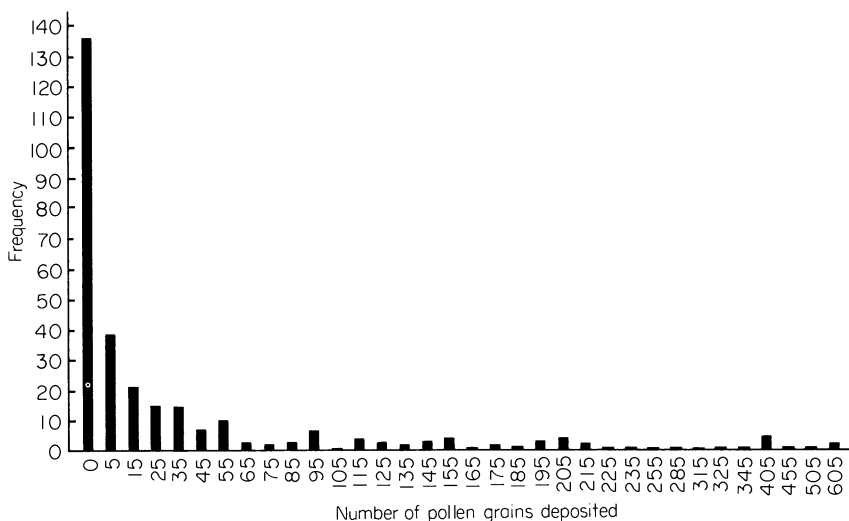


FIG. 3. Frequencies of pollen deposition by individual moths on stigmas of virgin female flowers of *Silene vulgaris*. Interval is 10 and intervals containing no observations are omitted.

TABLE 1. Noctuid and sphingid moths captured on the flowers of *Silene vulgaris* during 1986–89, their proboscis lengths, the percentage that deposited pollen on stigmas (PD), the percentage of moths that deposited 150 pollen grains or more (PD $\geq$ 150), the mean number of pollen grains deposited, and the total and relative deposition of pollen grains during the period. Unidentified moths escaped after flower visitation. The nomenclature of moths follows Svensson (1987).

Species	Proboscis length (mm)		Numbers collected				PD (%)	PD $\geq$ 150 (%)	No. of pollen grains (mean $\pm$ S.D.)	Pollen grains deposited	
	mean $\pm$ S.D.	n	1986	1987	1988	1989				Total	%
1. <i>Apamea furva</i> (D. & S.)	11.0 $\pm$ 0.5	42	16	17	19	2	43	6	83 $\pm$ 144	1904	14
2. <i>Diachrysis chrysis</i> (L.)	15.7 $\pm$ 0.8	37	31	1	12	1	75	18	93 $\pm$ 119	3138	23
3. <i>Cucullia umbratica</i> (L.)	20.3 $\pm$ 0.6	25	1	1	3	33	55	16	78 $\pm$ 75	1630	12
4. <i>Autographa gamma</i> (L.)	16.5 $\pm$ 0.9	20	2	2	22	5	58	0	17 $\pm$ 29	306	2
5. <i>Deilephila porcellus</i> (L.)	18.3 $\pm$ 1.0	9	9	0	0	6	53	27	178 $\pm$ 179	1415	10
6. <i>Hadena perplexa</i> (D. & S.)	12.4 $\pm$ 1.0	61	6	2	5	1	64	7	62 $\pm$ 61	555	4
7. <i>Apamea monoglypha</i> (Hufn.)	13.0 $\pm$ 0.6	12	1	1	7	2	45	0	15 $\pm$ 20	74	1
8. <i>Autographa pulchrina</i> (Hufn.)	17.0 $\pm$ 0.8	9	8	0	2	0	30	0	53 $\pm$ 76	159	1
9. <i>Hadena confusa</i> (Hufn.)	14.6 $\pm$ 0.8	27	1	2	5	1	78	0	30 $\pm$ 25	211	2
10. <i>Autographa jota</i> (L.)	17.7 $\pm$ 0.2	4	2	0	1	5	50	12	91 $\pm$ 152	364	3
11. <i>Hadena rivularis</i> (F.)	11.6 $\pm$ 0.6	21	4	0	1	0	0	0	0	0	0
12. <i>Apamea subulstris</i> (Esp.)	11.2 $\pm$ 0.7	5	0	1	3	0	75	0	50 $\pm$ 10	150	1
13. <i>Cucullia lychnitidis</i> Ramb.	21.0 $\pm$ 1.1	4	3	0	1	0	75	0	48 $\pm$ 29	144	1
14. <i>Autographa bractea</i> (D. & S.)	19.7 $\pm$ 0.5	3	2	0	0	2	25	0	1	1	0
15. <i>Polia bombycina</i> (Hufn.)	12.9 $\pm$ 0.3	4	0	3	1	0	50	50	137 $\pm$ 159	274	2
16. <i>Abrostola triplasia</i> (L.)	12.3 $\pm$ 1.1	2	2	0	0	1	67	50	270 $\pm$ 184	543	4
17. <i>Hadena bicruris</i> (Hufn.)	22.9 $\pm$ 1.3	23	0	1	1	1	33	0	10	10	1
18. <i>Apamea lateritia</i> (Hufn.)	16.8 $\pm$ 0.5	2	0	1	1	0	100	50	115 $\pm$ 120	230	2
19. <i>Autographa festucae</i> (L.)	14.2 $\pm$ 0.4	2	1	0	1	0	100	0	28 $\pm$ 30	56	1
20. <i>Agrotis segetum</i> (D. & S.)	10.5	1	0	0	1	0	0	0	0	0	0
21. <i>Apamea lithoxylea</i> (D. & S.)	11.5	1	0	0	0	1	0	0	0	0	0
22. <i>Mniotype adusta</i> (Esp.)	12.0	1	0	0	1	0	100	0	15	15	1
23. <i>Cucullia absinthii</i> (L.)	14.5	1	0	1	0	0	100	0	11	11	1
24. <i>Hyles galii</i> (Rott.)	25.5	1	0	0	0	1	0	0	0	0	0
25. <i>Hada nana</i> (Hufn.)	10.5	1	0	1	0	0	100	100	600	600	4
26. <i>Noctua pronuba</i> (L.)	—	0	1	0	0	0	0	0	0	0	0
Not identified	—	0	20	2	0	2	69	2	110 $\pm$ 89	1822	13
Year											
1986	14.7 $\pm$ 3.1	78	110				55	11	98 $\pm$ 119	6989	43
1987	13.1 $\pm$ 3.4	28		36			54	13	128 $\pm$ 68	2488	18
1988	14.2 $\pm$ 3.1	74			87		68	7	52 $\pm$ 94	3076	22
1989	18.9 $\pm$ 3.2	36		36		64	49	11	74 $\pm$ 98	2320	17
1986–89	15.0 $\pm$ 3.6	216	110	36	87	64	57	10	81 $\pm$ 36	13612	100

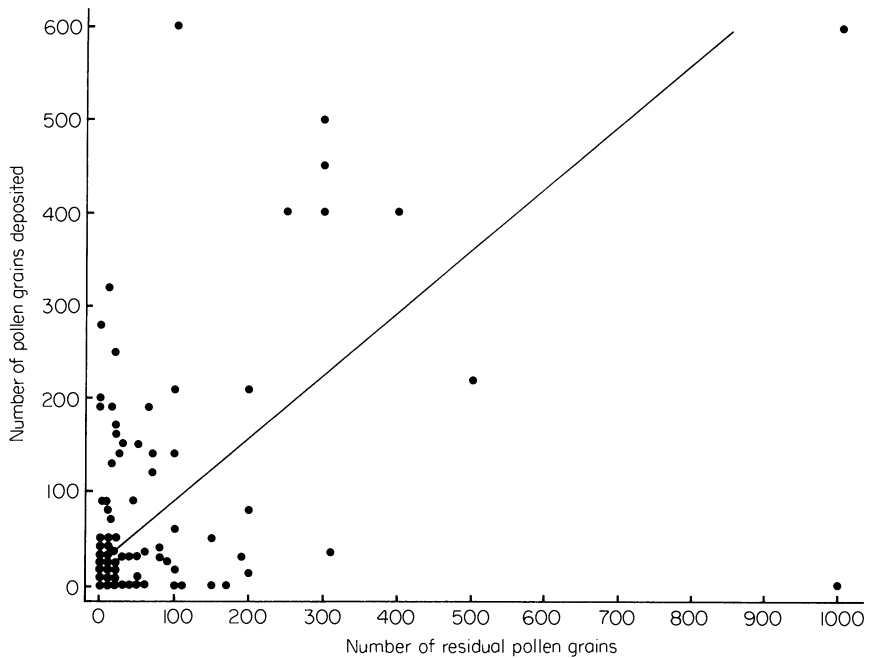


FIG. 4. Relation between the number of residual pollen grains on moth bodies and the number of pollen grains deposited by individual moths on virgin stigmas of female *Silene vulgaris* flowers. The line denotes the linear regression $y = 24.1 + 0.67x$, the data point at 1000 residual pollen grains and 0 deposited pollen grains being excluded from the calculation.

There was no significant difference in pollen deposition between the first (95 ± 155 , $n = 44$) versus the second (83 ± 156 , $n = 44$) nor between the first (89 ± 128 , $n = 15$) versus the third (83 ± 147 , $n = 15$) flower visits for those moth individuals for which serial data could be collected (Wilcoxon matched-pairs signed-ranks tests, $P > 0.05$).

The numbers of pollen grains deposited differed significantly only between the best (1987) and the poorest (1988) year (Table 1; Wilcoxon rank-sum tests, $P < 0.05$). Four species, *Apamea furva*, *Diachrysia chrysitis*, *Cucullia umbratica* and *Deilephila porcellus*, accounted for 69% of the total number of pollen grains deposited. Among the six most-frequent visitors, *Autographa gamma* deposited a significantly lower number of pollen grains than any of the other species (Table 1; Wilcoxon rank-sum tests, $P < 0.05$). No other significant differences between species in this respect were observed, but more samples could have shown that the sphingid moth *Deilephila porcellus* was a more efficient pollinator. The seed predatory *Hadena* moths were not especially abundant or efficient pollinators: *H. perplexa*, *H. confusa*, *H. rivularis* and *H. bicruris* together accounted for only 7% of the total number of pollen grains deposited (Table 1). The median number of pollen grains deposited during one flower visit by the most frequent moth species and their estimated 'one visit' contribution to seed set in female *S. vulgaris* is shown in Fig. 2. The number of seeds predicted from the median score in pollen deposition in one visit by moths in 1986 and 1987 was 28 and 32, respectively, which was much lower than the natural seed set in the same years (Fig. 2).

Time-related factors and pollen deposition

In 1986, the abundance of flower visiting moths was relatively high during the late part of the flowering season, when pollen availability was decreasing. As expected, the number of pollen grains deposited on stigmas by moths decreased significantly during the observation period in 1986 ($r = -0.35$, $n = 112$, $P < 0.001$). Conversely, few moths were present late in the flowering in 1987–89, and no negative correlation ($r = 0.02$, $n = 34$; $r = 0.02$, $n = 92$; and $r = -0.01$, $n = 65$, respectively) was found between pollen deposition and date in these years. In 1986, *Apamea furva* delivered pollen only at 19% of its visits ($n = 16$) compared to 47% in 1987 and 58% in 1988, when the species also was abundant. In 1986, *A. furva* became abundant at the end of the flowering period when access to pollen was on decline. On the other hand, in 1987 and 1988, *A. furva* appeared relatively earlier in relation to *S. vulgaris* than in 1986. However, the yearly proportions between pollination and visitation were not statistically different ($\chi^2_2 = 3.3$, $P = 0.2$).

Time of the visit in the evening did not affect the amount of pollen deposited for all species combined ($r = 0.08$, $n = 165$, $P = 0.27$) or for species 1, 3 and 4 in order of abundance ($r = -0.15$, $n = 35$, $P = 0.39$; $r = 0.16$, $n = 17$, $P = 0.53$ and $r = 0.03$, $n = 26$, $P = 0.89$, respectively). However, for the noctuid moth *Diachrysia chrysitis* there was a positive correlation ($r = 0.50$, $n = 21$, $P < 0.05$), i.e. pollen deposition became higher as the evening proceeded.

Moth behaviour and pollen deposition

The mean time spent by a moth at a flower was 19 ± 10 seconds ($n = 136$), which may have been longer than usual because the flowers had been bagged. There was no significant difference between species, the means being 21 ± 9 ($n = 18$), 22 ± 8 ($n = 10$), 18 ± 9 ($n = 33$) and 18 ± 9 ($n = 26$) seconds, respectively, for the four most abundant visitor species (ANOVA, $F = 1.07$, $P = 0.37$), and no significant relationship between foraging time at a flower and pollen deposition ($r = 0.11$, $P = 0.19$, $n = 131$).

Four major types of foraging behaviour were recorded; landing and sitting (small noctuids), landing and hanging from the flower (large noctuids), fluttering while sitting (the *Plusiinae* noctuids, i.e. *Diachrysia* and *Autographa*), and hovering without landing (hawkmoths). No significant differences were observed between these behavioural types in terms of quantity of pollen deposited, the means being 93 ± 128 ($n = 27$), 53 ± 63 ($n = 27$), 69 ± 123 ($n = 33$) and 178 ± 179 grains ($n = 8$), respectively (Kruskal–Wallis test, $P = 0.27$).

Morphology and pollen deposition

There was no significant overall correlation between number of pollen grains deposited and proboscis length ($r = 0.01$, $n = 110$, $P = 0.95$), even when the mean numbers of pollen grains were tested for association with moths within different proboscis length intervals (Fig. 5; $r = -0.57$, $n = 7$, $P = 0.18$). Also, no significant correlations appeared between proboscis length and number of deposited pollen grains for the four most common species ($r = 0.05$, -0.09 , -0.09 and -0.07 , respectively). However, in nine of the thirteen cases where visiting moths with high load of pollen failed to deposit any pollen at all the moths had a proboscis length

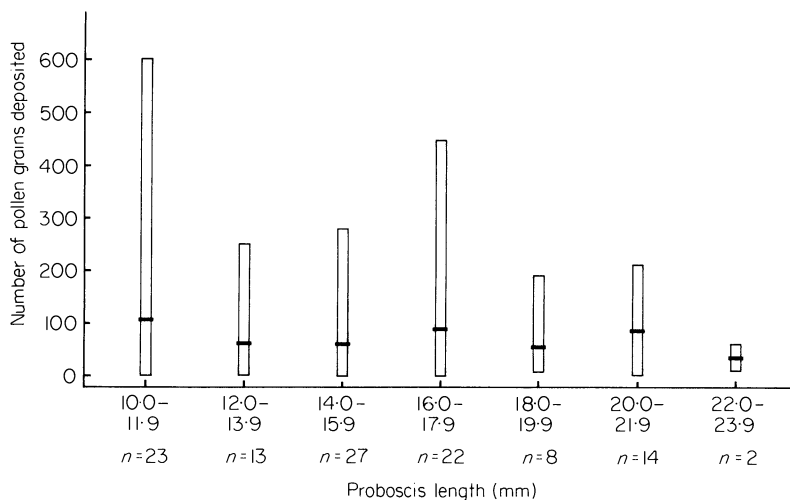


FIG. 5. The range (box) and mean (tick mark) number of pollen grains deposited on stigmas of *Silene vulgaris* in relation to moths grouped by proboscis length.

of 17 mm or more, a number significantly greater than the expected number from relative abundance of 3.4 (26% of all visiting moths had a proboscis ≥ 17 mm long; $\chi^2_1 = 12.6$, $P < 0.001$).

Corolla depth (mean ± 1 S.D.) was 10.4 ± 0.89 mm ($n = 42$) in flowers on female individuals, 10.5 ± 0.84 mm ($n = 19$) in male-phase flowers and 10.7 ± 0.90 mm ($n = 19$) in female-phase flowers on hermaphrodite individuals. The differences were not statistically significant (Tukey's HSD test, $P > 0.05$). However, the stamens of male-phase flowers were significantly shorter (18.5 ± 0.81 mm, $n = 20$) than the styles of female-phase flowers on hermaphrodite or female individuals (20.1 ± 1.72 mm, $n = 19$ and 19.8 ± 1.42 mm, $n = 19$, respectively; Tukey's HSD test, $P < 0.05$). The number of pollen grains deposited was not correlated with corolla depth or style length, either for all moths taken together ($r = -0.09$, $n = 105$, $P = 0.34$ and $r = -0.02$, $n = 30$, $P = 0.88$, respectively) or for species 3 and 4, for which sufficient sample sizes were available for analysis ($r = -0.08$, $n = 32$, $P = 0.66$ and $r = 0.18$, $n = 32$, $P = 0.30$, respectively for *Cucullia umbratica*, and $r = 0.20$, $n = 19$, $P = 0.41$ for style length and *Autographa gamma*).

DISCUSSION

By comparing the number of seeds predicted from the median pollen deposition score with the number of seeds obtained by maximum experimental pollen deposition and the numbers found in capsules of individuals in the surrounding *S. vulgaris* population, it is clear that many flowers have to be visited more than once to obtain a full seed-set. The flower visitation and pollen deposition results show that the local population of *S. vulgaris* was pollinated by a guild of moths, in which all important pollinator species varied greatly in abundance from year to year. Pollinator guild composition probably also varies within seasons. If the relative contribution to plant

fitness by different pollinators fluctuates, any evolutionary trends towards specialization should be diffuse or nonexistent (Morse & Fritz 1983).

The frequency and number in pollen deposition show that no moth species stands out as especially dominant or efficient as a pollinator. Most of the moth pollinator species of *S. vulgaris* visit a broad spectrum of plant species (Knuth 1898; Wahlgren 1941). Relying upon generalistic insects may be hazardous for a plant because generalists are seldom efficient pollinators as they may shift between plant species and waste much pollen (cf. Campbell 1985). In the present study the noctuid *Autographa gamma* was a particularly inefficient pollinator, making 10% of all visits but depositing only 3% of all pollen delivered (Table 1). Indeed, this moth is known as an extreme generalist (Schremmer 1941; Wahlgren 1941). Even the large stands of *S. vulgaris* flowers may not have been enough to keep *A. gamma* flying between conspecific plants, but much of the pollen removed by this moth may have been wasted before reaching fertile destinations. Mass flowering, as shown by *S. vulgaris* (Pettersson 1991), will be selected for when relying on inconstant pollinators.

Several well known cases show that ovipositing insects give rise to more seeds by pollination than are consumed by their larvae: *Yucca*–*Tegeticula* moths (Powell & Mackie 1966), *Ficus*–agaonid wasps (Wiebes 1979), and *Trollius*–*Chiastocheta* flies (Pellmyr 1989). In the *Silene*–*Hadena* system, however, the present results show that, although the *Hadena* moths are in a position to influence their larval food resource through pollination, they act as relatively poor pollinators. In *S. vulgaris* on average twenty-one seed capsules are consumed per *Hadena* larva, a loss which creates a strongly negative balance for a plant which harbours the parasitic *Hadena* moths as pollinators (Pettersson 1991). Thus, the *Hadena* moths largely depend on other moths' pollination activities.

In contrast to plants with long corolla tubes which only allow moths with certain proboscis lengths to reach the nectar, *S. vulgaris* has not only a short corolla, but also an elastic corolla-mouth, and the stigmas and anthers protrude on bendable styles and filaments, respectively. These traits allow short-tongued as well as longer-tongued moths to reach the nectar while they may all, as shown by the present results, play a role as pollinators. Differences in length of styles and stamens evidently reflect a 'functional overlap', the somewhat longer styles promoting pollen receipt by reaching beyond and thus raking through the pollen pool placed on the moths by the somewhat shorter stamens. Almost all anthophilous noctuid moths in western Europe have proboscis lengths within the range of 10–20 mm (Knuth 1898; Nilsson 1978). As shown by the present study, lengths in this range all allowed pollination, but the most long-tongued moths were less efficient in *S. vulgaris*. Only one visit by a moth species with a proboscis longer than the floral sexual organs (the hawk moth *Hyles galii*) was recorded. However, the long-tongued hawk moth *Hyloicus pinastri* (L.) (proboscis length c. 30 mm) has frequently been encountered as a flower visitor in *S. vulgaris* populations in central Sweden (L. A. Nilsson, personal observation). Such relatively long-tongued moths may play a minor role as pollinators and a major role as nectar thieves as they hover well outside the floral sexual organs while extracting the nectar (cf. Nilsson 1978, 1988).

Moths usually visited a series of flowers on the same female *S. vulgaris* individual, but no difference in terms of size of pollen deposition was statistically detected between the first, second or third flowers in order of visitation by individual moths. Later in a sequence the number of pollen grains deposited must decrease because

the insect's pollen store is not replenished from the unisexual flowers (cf. Thomson & Plowright 1980; Waser & Price 1982, 1984; Thomson *et al.* 1986; Svensson 1985; Waser 1988).

The number of seeds capsule⁻¹ in the female plants equalled the number of seeds produced in capsules of hermaphroditic individuals, a result obtained also in other studies of *S. vulgaris* (Dulberger & Horovitz 1984; Jolls 1984). Therefore, although the present study focused on female individuals, the numbers of seeds set will probably be similar for hermaphroditic individuals. Jolls & Chenier (1989) reported that seeds from out-crossed hermaphrodites were more likely to germinate than those from females, which, in turn, were more likely to germinate than those from selfed hermaphrodites.

The study also illustrates methodological problems. Pollen grains may fall off during capture of the moths, a fact that should be considered when basing studies in pollination on counts of pollen on insect bodies. This is the obvious reason why the regression line in Fig. 4 does not pass through the origin. Furthermore, the present study does not consider the possibility that different moths may remove different amounts of pollen from the anthers but deposit the same amounts on stigmas.

The novel information suggests a certain evolutionary history of the weed *S. vulgaris*. Variation in pollinator species in its original habitats could have favoured flowers that could be pollinated by various moth species, so that *S. vulgaris* may have been pre-adapted to act as a successful opportunist when man-influenced vegetation and soil disturbance became frequent. As the plant utilized a large variety of moth species as pollinators it was in a position to overcome the unpredictability that may have existed at a given locality, even with a gynodioecious breeding system—a quite impressive achievement because most typical weeds are autogamous. To summarize, a changing pool of pollinator species and lack of variation among pollinators in pollination efficiency are factors that probably oppose specialization and interdependence between a plant species and particular pollinator species. Such a set of factors may be responsible for the evolution of the plastic floral traits and pollination system in *S. vulgaris*, so that it may function with the moth fauna in virtually any colonizable area.

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