Temporal changes in pollen flow and neighbourhood structure in a population of *Saxifraga hirculus* L.

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Summary. The population area of flowering shoots of the perennial herb, *Saxifraga hirculus*, reaches a max. of 134 m² and an overall density of flowers/m² of 11.4. The flower is mainly visited by a syrphid sp., *Eurimyia lineata*, and to a lesser extent by another syrphid *Neoscia tenur*, a moth, *Zygaena trifolii*, and a fungus gnat, *Asindulum nigrum*. The distribution of the interfloral flight distance is leptokurtic. The mean flight distance of the visitors is 101 cm. 10% of the flights are much longer (2-8 m: cross-flower patch, and about 20 m: cross-population flights). If they are not included, the mean of flights (<1.7 m) becomes 28 cm. These flights become shorter with increasing flower density. The visitors do not have a nearest-neighbour foraging pattern. They visit on average the 8th nearest neighbour. The distribution of flight directions is uniform. Seed dispersal distances have a leptokurtic distribution and a mean dispersal distance of 13 cm. The ecological neighbourhood area is 66.4 m² and 64.9 m² assuming normality and allowing for leptokurtosis. *Z. trifolii* with its large proportion of long flights increases the size of the neighbourhood area considerably. The mean flight distance (<1.7 m) is correlated with neighbourhood area. The evolutionary impact of moths and butterflies to plant population structure is stressed.

Key words: Cross-population flights – Ecological neighbourhood – Flower foraging – Syrphidae – *Zygaena trifolii*

Gene flow, mating system, and effective population density strongly influence genetic differentiation in plant populations and have received much attention in relation to the concept of genetic neighbourhood (Schaal and Levin 1978; Crawford 1984). Gene flow happens via pollen and seeds. Pollen flow is estimated in several ways, but measuring pollinator flight distances has been the predominant method (Kerster and Levin 1968; Levin and Kerster 1968; Schaal and Levin 1978; Beattie and Culver 1979; Schmitt 1980, 1983; Waser 1982; Zimmerman 1982). Effective gene flow via pollen has been shown to be greater than would be inferred from pollinator movement alone (potential gene flow *sensu* Rai and Jain 1982) (Schaal 1980; Handel 1983). This may often be explained by pollen carry-over, i.e., trans-

port of pollen from a flower and further than to the next flower visited (Levin and Berube 1972; Primack and Silander 1975; Handel 1976; Thomson and Plowright 1980; Waser and Price 1982, 1984; Crawford 1984). Pollen carry-over is among other things determined by the number of flowers visited per plant and the degree of flight directionality of the flower visitors (Levin et al. 1971; Pyke 1978a, 1978b).

Pollinator flight distance is related to plant spacing (Beattie 1976; Schmitt 1983). Most flower foragers have short flight distances, with most flights occurring between near-neighbours (Pyke 1978a; Schaal 1978, 1980; Waddington 1981). In general, distributions of pollinator flight distances are strongly leptokurtic.

The theory of flower foraging behaviour is bee- and hummingbird-biased with the exception of a few studies of butterflies (e.g., Levin and Berube 1972; Schmitt 1980) and flies (e.g., Beattie 1976; Schmitt 1983).

Different pollinator species may differ in flight pattern and amount of pollen transferred and thus have differential impact on pollen flow and neighbourhood structure of a given plant species (Linhart 1973; Schmitt 1980; Murawski and Gilbert 1986). In some cases no differences in pollen movement between visitors have been found (Antlfinger 1982; Waser 1982). As is generally found, the density of flowers and the guild of flower visitors change through the season. Relatively few studies have, however, dealt with this aspect and its impact on gene flow and neighbourhood (e.g., Schemske et al. 1978; Waser 1978, 1979; Schmitt 1983).

The species in this study, *Saxifraga hirculus* L., is a perennial herb reproducing by seeds and spreading clonally by runners. The flowering shoot usually bears only one flower. Self-pollination is prevented by complete protandry. The species seems to be fully between-ramet compatible and partially within-ramet compatible. Its sexual natural history has been described in Olesen and Warncke (1989a, b). Although only one fly species is of major importance to *S. hirculus* pollination, a coterie of less frequent and less efficient visitors is suspected to have great impact upon neighbourhood structure and seed quality.

This study compares the pollen flow mediated by different types of pollinators throughout the flowering season in a population of *S. hirculus*, estimates seasonal changes in neighbourhood area and size and discusses the genetic and evolutionary consequences to a plant population of different behaviour types of the pollinators.

Methods

From June 27 till August 17, 1984, field studies were conducted on the only major Danish population of *S. hirculus*: Rosborg Sø, a bog and helorheocrene spring area surrounded by heathlands situated in an extensive military area Finderup Øvelsesterræn, near Viborg, in Jutland ($56° 25'$ N, $9° 13'$ E). The general biology of Danish spring areas is described in detail in Warncke (1980).

Two small springs (a southern and a northern one) each 900 m^2 in size contained *S. hirculus*. The northern one (some 30 metres square) was used in this study. It possessed the majority of the flowering shoots.

Each day was divided into three observation intervals: 6-noon, 1–5 p.m. and 6–8 p.m. European Summer Time, i.e. 2 h ahead of GMT. The time 6 a.m. to 8 p.m. was the main period of activity of the pollinators.

All flowers were tagged and mapped the day they opened. The study population was divided into squares of 1 m^2 each. The "pollination" area of the population of flowers was calculated as the number of squares containing at least 1 flower. Mean number of flowers per shoot was 1.7. The majority of flowering shoots bore only one flower at a time. Squares without flowering shoots were only included, if they were surrounded by flower-containing squares on at least 3 sides. This was chosen as the procedure since the average flight distance was 1 m (see later Table 1). If all the area used by pollinators making interfloral flights was included the area of the population would increase by at least 43 m^2 (see later Fig. 1).

Many different insects forage in the flowers of *S. hirculus*, 50%, 16%, 9%, 6%, and 19% of all visits are made by *Eurimyia lineata* (Fabr.) (Diptera: Syrphidae), *Asindulum nigrum* Latreille (Diptera: Mycetophilidae), *Neoascia tenur* (Harris) (Syrphidae), *Zygaena trifolii* Esper (Lepidoptera: Zygaenidae), and other insects (Coleoptera, Diptera, Lepidoptera) resp. Foraging is defined here as the active removal of pollen and/or nectar or the probing of flower structures with mouthparts. Visitors were observed throughout the day and season. Individual flower visitors were observed as long as possible while they were foraging and the number of visited flowers was noted. Most observations were made in a 2×2 m plot in the centre of the population, although all flights out of this plot were followed as long as possible. Since the distribution of open flowers was patchy the flights were classified as intra-flower patch, cross-flower patch and cross-populational, i.e. from one margin of the population to another. Later the flight distance between 2 successive visits and the angle of departure from the middle flower of each triplet of flowers visited was estimated (the angular deviation). These angles ranged from $-180°$ to $+180°$ with $0°$ indicating a move straight ahead. Pairs of turns were χ^2-tested corrected for continuity to see if right and left turns were associated with one another. The foraging runs of individual insects were examined to see if insects revisited individual flowers. All flowering stems within a circle with flight distance as radius and the flower of departure as centre were counted as bypassed by the insects. The percentage of insect moves to each nearest neighbour was then tabulated.

Seed dispersal was measured in the spring area using a gross-woven blanket covered by a net to protect seeds from birds.
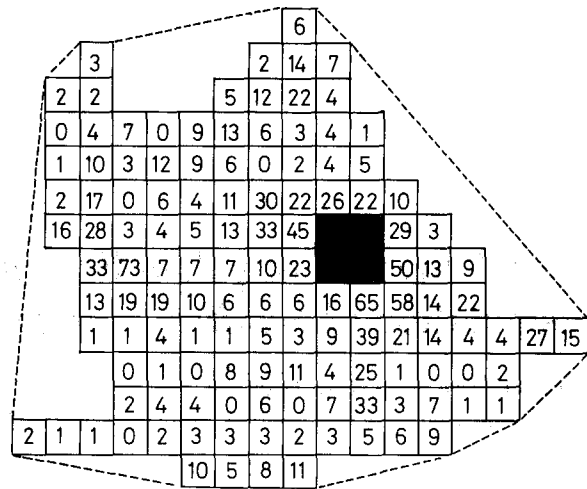

Fig. 1. Map showing the spatial extent of the flower population of *S. hirculus*. Each square is of a size of 1 m^2. The numbers are the summation of all open flowers during the whole season in each square. The $2 \times 2 \text{ m}^2$ square is the observational plot. All the area included by the dotted line may belong to the area of the population, since the marginal areas are crossed by interfloral flying insects
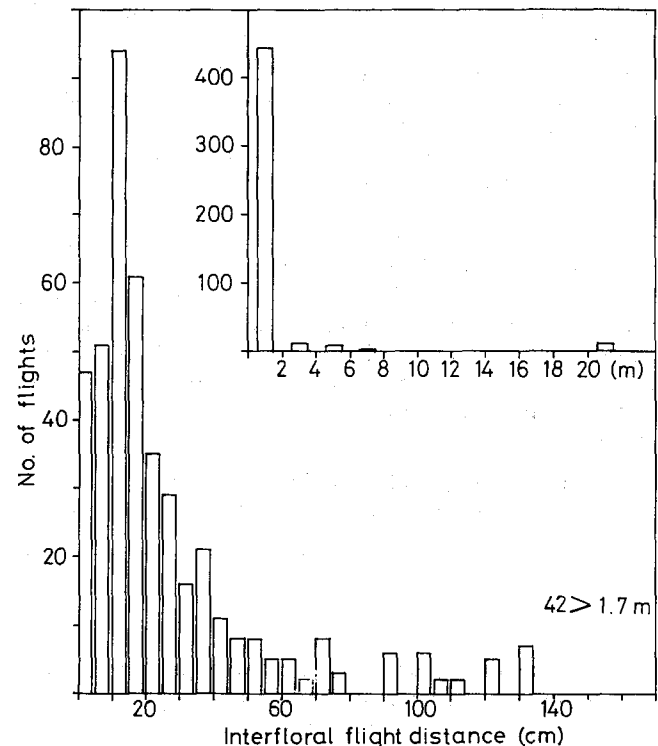

Fig. 2. The distribution of distances flown by flower-visiting insects between successively visited flowers of *S. hirculus* (Observation period: July 10–29; flower-visiting *Meligethes* spp. are excluded from the material)

Results

During the season the number of flowers in the population reached a total of 1525 (Fig. 1). The area of the flowering population was 134 m^2 and the overall density, $d \pm$ SD, of flowers/m^2 was 11.4 ± 14.2 (range 1–73). The spatial distribution of flowers was very clumped (July 17: CD = 12.8139,

Table 1. The relation between interfloral flight distance of visitors to flowers of *S. hirculus* and time of season. The flight distances fall into three classes (Fig. 2). No flights 1.35–2 m long and 8–about 20 m long were observed

Date in July	Flight distance (cm)		
	intra-patch (<170 cm)	intra- and cross-patch (<about 8 m)	all incl. (<about 20 m)
11	38±36 (N= 11)	64± 97 (N= 12)	64± 97 (N= 12)
17	34±33 (N= 35)	45± 58 (N= 37)	236±590 (N= 41)
18	29±29 (N=142)	54±100 (N=154)	103±322 (N=158)
19	27±27 (N=155)	45± 93 (N=163)	92±314 (N=167)
24	24±23 (N= 21)	63± 59 (N= 23)	63±159 (N= 23)
25	19±10 (N= 30)	34± 87 (N= 31)	34± 87 (N= 31)
26	14±11 (N= 19)	59±106 (N= 23)	59±106 (N= 23)
Mean±SD	28±28 (N=413)	49± 91 (N=443)	101±307 (N=455)

Table 2. The relation between interfloral flight distance of the different visitors to flowers of *S. hirculus* and time of season. (Flight distances classes, see Table 1)

Date in July	Flight distance (cm)		
	intra-patch (<170 cm)	intra- and cross-patch (<about 8 m)	all incl. (<20 m)
Eurimyia lineata			
17.–19.	29±29 (N=223)	46± 81 (N=237)	62±196 (N=239)
24.–26.	22±16 (N= 36)	46± 82 (N= 40)	94±316 (N= 41)
Neoascia tenur			
17.–19.	30±27 (N= 13)	30± 27 (N= 13)	170±527 (N= 14)
24.–26.	23±35 (N= 12)	23± 35 (N= 12)	23± 35 (N= 12)
Asindulum nigrum			
17.–19.	20±18 (N= 21)	76±186 (N= 23)	76±186 (N= 23)
24.–26.	20±26 (N= 13)	35± 58 (N= 14)	35± 58 (N= 16)
Zygaena trifolii			
17.–19.	30±29 (N= 42)	83±128 (N= 51)	222±517 (N= 55)
24.–26.	has almost disappeared as imago late in July		
Other visitors (mainly 14 Syrphidae spp.)			
17.–19.	32±30 (N= 44)	32± 30 (N= 44)	46±407 (N= 46)
24.–26.	18±11 (N= 9)	18± 11 (N= 9)	18± 11 (N= 9)

$G_{adj} = 127.71 \gg \chi^2_{0.001} = 16.27$; August 4: $CD = 8.91$, $G_{adj} = 166.04 \gg \chi^2_{0.001} = 27.88$, Poisson distr., Sokal and Rohlf 1981), i.e., the flowers were found in patches.

The distribution of interfloral flight distances was leptokurtic (Fig. 2). Kurtosis was 5.0***. Most of the moves were very short. 87% were less than 80 cm. Flight distance averaged 101±307 cm (Table 1). If the 12 cross-population flights (about 20 m long) observed were excluded the flight distance averaged 49±91 cm. If the 30 cross-patch flights (1.7–8.0 m) were excluded too the flight distance (intra-patch) averaged 28±28 cm (N=413), i.e., a few cross-patch and cross-population flights increased mean length considerably.

In general, intra-patch flights became shorter through the flowering season (N=413, $b = -1.477$, $t_s = 6.967$, $P < 0.001$), while flight distance (cross-patch flights incl. and cross-population flights incl. resp.) did not decrease through season (N=443, $b = -0.512$, $t_s = 0.569$, $P > 0.2$; and N= 455, $b = -4.686$, $t_s = 0.903$, $P > 0.4$, resp., Table 1).

Table 2 gives the flight distances of the main visitors in relation to season. Early in the flowering season the intra-patch flights of *A. nigrum* were significantly shorter than for the other visitors ($P < 0.05$); later in the season this difference disappeared, since the other visitors now made shorter flights. The intra-patch flights became significantly shorter through season in *E. lineata* ($t_s = 2.102$, $P < 0.05$) and in the group 'Other visitors' ($t_s = 2.414$, $P < 0.05$), but not in *N. tenur*. However, the change in *N. tenur* was close to the 5% significance level ($t_s = 2.147$).

Excluded from the data above were flights where the insect returned to the same flower: that is 1%, 7%, 30%, and 5% of all flights of *E. lineata, N. tenur, A. nigrum*, and *Z. trifolii* resp. *A. nigrum* and *Z. trifolii* often crawled or flew from the interior of the flower and down to the
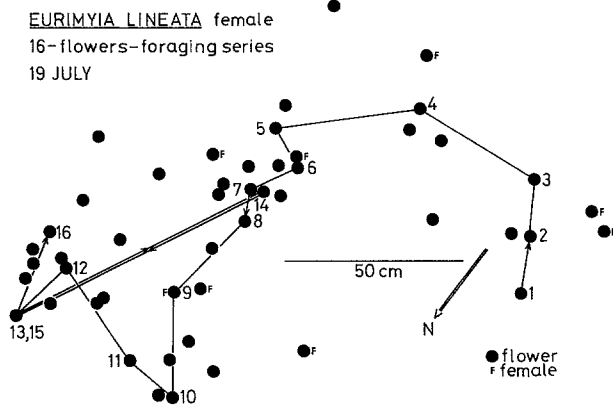
Fig. 3. An example of a foraging tour of an *E. lineata* female visiting flowers of *S. hirculus*

Fig. 4. Polar wedge diagram showing the distribution of flight directions of all visitors of *S. hirculus*

underside of the flower and then returned to the interior. *N. tenur* flew up from the interior of the flower, hovered a few cm above it and then returned to the interior. These behavioural types were here regarded as one visit (with interruptions due to over-contamination with pollen, over-ingestion or to predator stimuli?) and not as a series of visits.

2.6% of all flights were across the population: that was 1%, 4%, 5%, and 7% of the flights of *E. lineata*, *N. tenur*, *A. nigrum*, and *Z. trifolii* resp. The proportion of cross-population flights of *Z. trifolii* was significantly higher ($P < 0.05$) than in the other species.

For every interfloral flight the density of flowers within a circle with the departure flower as centre and the interfloral flight distance as radius was calculated. All neighbours closer than the actual one visited were included since the flight directionality was demonstrated to be random (see later) and since the insects often crawled to the tip of the petal and then took off in a presumably unpredictable direction. Thus no obvious reason existed to exclude part of the circle around a flower. We found a negative regression between density and distance flown (only intra-patch flights) by three of the four major visitors (*E. lineata*: $b = -0.0002$, $t_s = 4.326$, $P < 0.001$; *N. tenur*: $b = -0.0003$, $t_s = 2.642$, $0.05 > P > 0.02$; *Z. trifolii*: $b = -0.0005$, $t_s = 4.315$, $P < 0.001$; and *A. nigrum*: $b = -0.0001$, $t_s = 1.163$, $P > 0.2$). Thus the intra-patch flight length was density-dependent for all visitors except for *A. nigrum*. In general, the visitors did not fly to the nearest neighbour: *E. lineata* flew to neighbour number 8.0 ± 7.8 ($N = 190$, range 1–45), *N. tenur* to 8.0 ± 7.0 ($N = 11$, range 1–20), *Z. trifolii* to 7.8 ± 8.8 ($N = 22$, range 1–32), and *A. nigrum* to 8.2 ± 8.1 ($N = 25$, range 1–31). Later in the season *Z. trifolii* disappeared as pollinator. The variance of the intra-patch flight distances decreased too with increasing flower density (Tables 1, 2).

In Fig. 3 an example of a foraging tour of an *E. lineata* is shown. Does this fly and the other visitors of *S. hirculus* show any directionality in their foraging? The flight directions were grouped into N, NE, E, SE, S, SW, W, and NW and their distribution was represented as a polar wedge diagram ($N = 217$, Fig. 4). The mean direction vector had a length $r_c = 0.0427$ and a mean angle $v = 163°$; the angular deviation s_c was 79° according to statistics for empirical
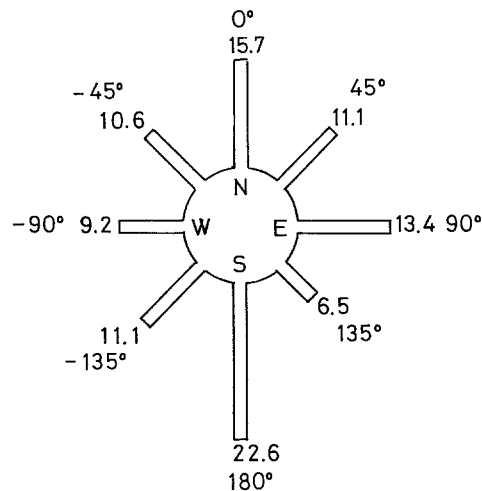
circular distributions (Batschelet 1965). The size of r is a measure of the dispersion of the directions. Much dispersion is indicated by a value of r close to 0. The maximum value of s_c was 81°. The distribution did not deviate significantly from uniformity, i.e., $r = 0$ ($z = 0.355$, Rayleigh test of randomness, Batschelet 1965). The distributions of the flight directions of *E. lineata*, *A. nigrum*, *N. tenur* and other visitors were all uniform, but *Z. trifolii* behaved differently ($N = 21$, $r_c = 0.4745$, $v = 178°$, $s_c = 59°$, $z = 4.4911 > z_{0.01}$). *Z. trifolii* had a highly significant directionality towards S.

Directionality may also be achieved if the visitors alternate between left and right turns. The visitors of *S. hirculus* were not doing this ($N = 36$, $\chi^2 = 6.89$, df $= 3$, $P > 0.5$). The sample sizes were too small to test each of the visitors.

In 17% of the flight tours observed, the insect returned to the same flower after having visited 0–5 other flowers. Three *E. lineata* were observed to revisit a flower after 7, 9 and 13 other flower visits, but these data were not included since we have very few data over long series of flower visits. Six%, 7%, 2%, 1%, 0%, and 1% of revisitation happened after 0, 1, 2, 3, 4 and 5 other visits resp. Thus after 2 other visits the chance of returning to the same flower was very small. Eleven%, 56%, 23%, 21% and 17% revisitation happened after 0–5 visits to other flowers in *E. lineata*, *A. nigrum*, *N. tenur*, *Z. trifolii*, and other visitors resp.

The distribution of seed dispersal distances was leptokurtic and mean dispersal distance was 13.2 ± 1.13 cm ($N = 189$).

Discussion

The shape of the distribution of interfloral flight distances resembles those reported from other studies (Kerster and Levin 1968; Levin and Kerster 1969; Pyke 1978a; Schaal and Levin 1978; Schmitt 1980). The relatively long mean flight distance found in *Z. trifolii* is in agreement with other studies of lepidopteran flight (Schmitt 1980). A minor portion of the flights of flower visitors is generally very long (Beattie 1976; Schmitt 1980; Waser 1982).

The interfloral flight distance is often used as an estimate of pollen flow distance. It is, however, obvious that a minor portion of pollen is being moved around in the

Table 3. The seasonal change in interfloral flight distance and variance of visitor groups of *S. hirculus* based on number of pollen visits during the first 75% (18.VII–3.VIII) of the pollination period (18.VII–10.VIII) (Olesen and Warncke 1989a)

Species	18.–21.VII (4 foraging days)					22.VII–3.VIII (8 foraging days)					18.VII–10.VIII (16 foraging days)				
	E	D	σ^2	g_2	α	E	D	σ^2	g_2	α	E	D	σ^2	g_2	α
E. lineata	9	62±196	3.84	5.7***	1.3	78	94±316	9.99	7.5***	1.4	90	91±304	9.24	6.2***	1.3
A. nigrum	0	76±186	3.46	–		2	35± 58	0.34	–		2	36± 60	0.36	2.0*	0.9
N. tenur	0	170±527	27.77	–		0	23± 35	0.12	–		1	89±255	6.50	4.2***	1.1
Z. trifolii	0	222±517	26.72	1.8*	0.8	0	–	–	–		0	222±517	26.72	1.8*	0.8
Others	1	46±407	16.56	–		5	18± 11	0.01	–		7	22± 66	0.44	1.5*	0.8
Average		66±227	5.15	4.1***	1.1		88±290	8.41	12.2***	1.7		85±283	8.00	5.0***	1.2
Total (%)	10					86									

E: Number of pollen visits in % to all open flowers during the period (see Table 4, Olesen and Warncke 1989b). *D*: Interfloral flight distance (cm), see Table 2. Average $D = E$ (with 2 dec.)$\cdot D/\Sigma E$; $D(18.\text{VII}–10.\text{VIII}) = \Sigma(E\ D)/E(18.\text{VII}–3.\text{VIII})$. σ^2: Variance of the flight distances (m²). g_2: Kurtosis of the distribution of flight distances. All show significant leptokurtosis (asteriscs). α: An estimate from the gamma function: $g_2 + 3 = \Gamma(\alpha)\Gamma(5\alpha)/\Gamma(3\alpha)^2$ (Beattie and Culver 1979). α originates from Bateman (1947), where it is the reciprocal value of the exponent in the exponential function describing the distribution of bee flight distances

Table 4. The seasonal change in effective neighbourhood size of *S. hirculus* based on visitation frequency and variance of flight distribution of the different flower visitor groups during the first 75% (18.VII–3.VIII) of the pollination period (18.VII–3.VIII) (Olesen and Warncke 1989a)

Species	18.–21.VII (4 foraging days)				22.VII–3.VIII (8 foraging days)				18.VII–3.VIII (12 foraging days)			
	NA_k	NA_n	N_s	N_{eff}	NA_k	NA_n	N_s	N_{eff}	NA_k	NA_n	N_s	N_{eff}
E. lineata	23.0	(24.1)	697	426	58.7	(67.8)	1955	1849	55.4	(58.1)	1468	1080
A. nigrum		21.7	658	401		2.1	70	66	2.3	(2.3)	61	45
N. tenur		174.5	5287	3228		0.8	27	25	40.3	(40.8)	1068	786
Z. trifolii	170.5	(167.9)	5166	3154					170.5	(167.9)	4518	3325
Others		104.0	3151	1924		0.1	3	3	2.8	(2.8)	74	55
Average	32.0	(32.4)	970	592	46.0	(52.8)	1532	1449	48.8	(50.3)	1293	952

NA_k: Allowing for kurtosis the neighbourhood area NA_k (m²)$= 2^{2\alpha} > [\Gamma(2\alpha+1)\Gamma(\alpha)/\Gamma(3\alpha)]\cdot\pi\sigma^2$ (Beattie and Culver 1979); NA_k has only been calculated when larger samples are available. $NA_n = 4\pi(^1/_2\sigma^2_{pollen})$ (Crawford 1984) assuming a normal distribution of flight distances. Gene flow mediated through seeds was not included in Tabs 3–4, but $\sigma^2_{seed} = 1.28$ m². Thus $NA = 4\pi(^1/_2\sigma^2_{pollen} + \sigma^2_{seed}) = 4\pi(^1/_2 \cdot 8.00 + 1.28) = 66.4$ m². 24% of the total NA was thus caused by seed dispersal. N_s (neighbourhood size)$= NA_k(NA_n)\cdot d$, where d is number of open flowers per m² inside the 2×2 m² area of observation. 18.–21.VII: $d = 30.3$; 22.VII–3.VIII: $d = 33.3$; and 18.VII–3.VIII: $d = 26.5$. N_{eff} (effective neighbourhood size)$= NA_k(NA_n)\cdot d_{eff}$, where d_{eff} (effective number of open flowers per m²)$= 4N_m\cdot N_f/(N_m+N_f) + ^1/_2$ per m² (Crawford 1984); and N_m and N_f are numbers of open flowers in male and female phase resp. (Fig. 6, Olesen and Warncke 1989a). 18.–21.VII: $d_{eff} = 4\cdot24.8\cdot5.5/30.3 + ^1/_2 = 18.5$; 22.VII–3.VIII: $d_{eff} = 4\cdot12.3\cdot21.0/33.3 + ^1/_2 = 31.5$; and 18.VII–3.VIII: $d_{eff} = 4\cdot20.3\cdot 6.2/26.5 + ^1/_2 = 19.5$

population by carry-over and long flights influencing genetic structure and gene flow disproportionately.

The importance of pollen carry-over on gene flow is highly influenced by the degree of flight directionality. In general, bees have a very linear flight reducing the frequency of revisitation (Levin et al. 1971). In "rich" patches, however, they show less directionality (Heinrich 1979). Random foraging has indeed been shown to be the optimal strategy when no disadvantage is associated with staying in the same foraging area (Zimmerman 1979). The 11% revisitation in *E. lineata* had probably little negative effect to the fly, since it did not empty all open anthers or all five nectaries in one visit. To maximize the rate of energy harvesting an optimal foraging animal is expected to minimize interfloral flight distance (Pyke 1978a, 1978b). Since the visitors of *S. hirculus* on average visited the 8th nearest neighbour these animals did not seem to forage optimally. Their indi-

vidual fitness is, however, also influenced by other tasks performed while foraging: avoiding predators, mate-searching, and body-gleaning.

When a bee visits more flowers on an inflorescence its next flight direction becomes less directional. The visiting of several nectaries and anthers in a flower by a fly may be an analogous situation causing random flight.

Leaving a flower of *S. hirculus* all its visitors chose any direction with about the same probability. The variation in mean flight length influences the importance of pollen carry-over. Thus pollen carry-over caused by some of the visitors greatly influences pollen flow and neighbourhood area.

The few long flights made by the visitors were not just of great importance to the plant population but also to the foraging of the pollinators. They might be analogous to the linear flight pattern made by bees.

Mean flight distance and mean nearest neighbour distance between flowers are generally correlated (Levin and Kerster 1969; Beattie 1976; Pyke 1978a; Waddington 1979). In this study Z. trifolii foraged in a density-dependent manner. Generally, lepidopterans show no clear relationship with plant density (Beattie 1976).

Data on pollen visits (Olesen and Warncke 1989a, b) and variances of flight distance distributions (all flights included, Table 2) throughout the season were used to estimate the ecological neighbourhood. The flowering shoot is taken to be the "ecological" unit.

The visitors contributed differently to neighbourhood since they moved different amounts of pollen different distances.

Estimates of neighbourhood size and area are given in Tables 3-4 (for details and formulae see subtext to tables). The population was assumed to have no net displacement over generations. The difference between values assuming normality and allowing for kurtosis was of minor importance. The neighbourhood area, NA, for the whole season was about 50 m^2, i.e., the whole population consisted of less than 3 neighbourhoods. This figure hides, however, much variation.

If only the variance of the intra-patch flights was used to calculate NA (Tables 1, 2), flower density would be inversely related to NA. Thus if cross-patch and cross-population flights were excluded from the data, plant density might be a reasonable predictor of NA (Levin and Kerster 1969; Schmitt 1980). This was, however, only true for average-NA and E. lineata-NA, i.e., NA in a flower population specializing on E. lineata as its sole pollinator. N. tenur and A. nigrum increased the variances of their intra-patch flight distributions with season, and Z. trifolii disappeared late in season. E. lineata-NA (intra-patch flights only) decreased from 0.53 m^2 (18.-21.VII) to 0.16 m^2 (22.VII-3.VIII). The average-NA (intra-patch flights only) decreased from 0.60 m^2 (18.-21.VII) to 0.14 m^2 (22.VII-3.VIII). Cross-patch and cross-population flights increased E. lineata-NA (24.1:0.53=) 45 and 424 times early and late in season resp. Average-NA was increased 54 and 377 times resp. Thus the rare long flights of generally short-distance flyers must be very important to the population structure.

If Z. trifolii was the only pollinator, the whole population would be one neighbourhood early in the season (170.5>134). Although this insect sp. only mediated about 1% of all the pollen visits it increased NA from 23 m^2 to 32 m^2 (39%) (Table 4). NA has been shown to jump by an order of magnitude if less than 10% of the pollen transport is caused by butterflies (Schmitt 1980). Schmitt (1980) and this study suggest that a population becomes more genetically homogeneous if it shifts from bees to flies and to moth/butterflies as pollinators or incorporates these animals into its pollinator fauna to a higher degree, i.e., stronger selective pressures are required to maintain genetic differentiation in a lepidopteran pollinated population than in a fly- or bee-pollinated one. Thus in any plant population with a multispecies pollinator coterie a small proportion of lepidoptera-mediated pollen flow may have great evolutionary importance (Schmitt 1980). This and the suspected decrease in competition among pollen grains for fertilization (Olesen and Warncke 1989a) and the decrease in average-NA with season imply changes in the genetic quality of the seed and thus of fitness of the offspring.

The hypothesis about the genetic importance of lepidop-

terans as interneighbourhood pollen agents has little connection with the discussions of lepidopterans as long-distance, interpopulational pollen agents (Wiklund et al. 1979, 1982; Courtney et al. 1982, 1983; Tepedino 1983).

N_{eff} is given in Table 4. The population had a size of about one neighbourhood. The protandrous system produced smaller effective neighbourhoods early and late in season. Distant parts of the population were only 1-few neighbourhood diameters apart in S. hirulus. Thus the population should exhibit significant genetic homogeneity and inbreeding.

Studies of visitation frequency and size of surface pollen load on visitors have shown that the number of pollen visits and probably of seeds produced in the supposed generalist S. hirculus is dependent on a single pollinator species, i.e. E. lineata (Olesen and Warncke 1989a, b). On the other hand, this study suggests that ecologically unimportant pollinator species may play important evolutionary roles to the structure of the plant population due to their divergent flight behaviour.

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