

Weather Conditions During Nuptial Flights of Four European Ant Species

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Summary. In 1977, 1978, and 1979 nuptial flights of Lasius niger L., Lasius flavus F., Myrmica rubra L., and Myrmica scabrinodis Nyl. were observed on the island of Schiermonnikoog and in the area around Amsterdam. Weather conditions during these flights were determined using data from meteorological stations at Schiermonnikoog and Schiphol Airport. Significant differences were found concerning daytime, global radiation and relative humidity at the beginning of flights of Lasius niger, Lasius flavus, and Myrmica rubra; Myrmica scabrinodis had no defined preferences for these parameters. Wind velocity at 2 m of height was less than 1.7 m.s⁻¹ during all flights before 20 August. After that date all species tended to fly at higher wind velocities as well.

The calculated ranges for daytime, temperature, global radiation, relative humidity, and wind velocity appeared to be sufficient to characterize all nuptial flight occasions at Schiermonnikoog.

Micrometeorological measurements in typical habitats of different ant species revealed that during flights the air temperature at 20 cm above ground and the soil temperature at 5 to 7 cm below ground were about equal in the habitat of the flying species, but unequal in the neighbouring habitats of coexisting ants.

Introduction

Large amounts of energy and biomass are invested each year by mature ant colonies in their dispersal. Especially ants such as *Tetramorium caespitum* Latr. and several *Lasius* species, producing relatively large queens compared to the worker size, may expend an equivalent of up to 60% of the total worker biomass when the winged sexuals leave the colonies for their nuptial flights (Brian et al. 1967; Brian and Elmes 1974; Nielsen 1978). For other European ant species, values of between 5% and 20% were demonstrated (Brian 1972; Jensen 1978).

The nuptial flight periods may differ for each species, but mostly the high summer months are preferred by ants living in temperate regions (Kannowski 1959; Collingwood 1979). Anticyclonic weather conditions with low wind velocities are considered as optimal for nuptial flights (Brian 1965). In some papers on nuptial flights of ants (Kannowski 1959; Talbot 1959; Wilson and Hunt 1966) and termites (Nutting 1969), temperature and light intensity are indicated as major triggering factors. How-

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ever, this concept is poorly supported by detailed analyses of the specific environmental conditions during flights.

In this paper, observations on nuptial flights of four common ant species, Lasius niger L., Lasius flavus Fabr., Myrmica rubra L., and Myrmica scabrinodis Nyl., are classified and related to data on air temperature, soil temperature, global radiation, relative humidity, rainfall, and wind velocity at the beginning of and prior to these flights.

Methods

During the summer seasons of 1977, 1978, and 1979, field surveys were made on ant communities in different parts of the Dutch Wadden island Schiermonnikoog. It was demonstrated that *Lasius niger, Myrmica rubra*, and *Myrmica scabrinodis* are important pioneering species in a 20-year-old coastal plain (Boomsma and de Vries 1980). *Lasius flavus* appeared to be the most common ant in the older sand-dune grasslands.

In July and August permanent observations on the date and time of nuptial flights were made on Schiermonnikoog. Occasionally, *Lasius niger* flights in the Amsterdam area and the province of North Holland were observed. The nuptial flights were divided into three categories:

- 1. extensive (conspicuous flights synchronized over a large area)
- 2. local
- 3. interrupted (abortive flights because of deteriorating weather conditions).

Normally, male ants ascend earlier for nuptial flights than females. On Schiermonnikoog, males of both *Lasius* species were usually active on the soil surface before the first queens came out and *Myrmica* males were forming swarms above elevated objects or mounds. Sometimes, when flight conditions were suboptimal, only a few agitated or flying males, but no queens, were observed. Since evidence was found that the timing and synchronization of flights by males may be arranged primarily according to specific endogenous activity rhythms (McCluskey 1965), the actual takeoff of queens was considered the most consistent flight action to be triggered by weather conditions.

In consequence, the hour in which the first queens ascended was chosen as the beginning of a nuptial flight and so this time was primarily analysed for its environmental conditions. Data from meteorological stations at Schiermonnikoog and Schiphol Airport were used for this purpose. Data from a provisional station in the coastal plain in 1978 were occasionally used in case of local flights in this area.

For all nuptial flights observed, lower and upper limits for time, temperature, global radiation, relative humidity, and wind velocity were established for each of the ant species. All times are presented as Local Summer Time (LST), which is 2 h ahead of GMT. Temperature and relative humidity were determined at 1.5 m, and wind velocity at 2.0 m above ground.

A selection of hours fitting these limitations was made by computer for the period from 25 July to 1 September of the investigated years in order to establish the "determining value" of these parameter sets.

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In the coastal plain, micrometeorological measurements of temperature profiles were made at the top of a small sand dune (Lasius niger habitat) and two Festuca mounds (Myrmica habitat) at heights of 20, 5, 3, 1, 0, -1, -3, and -5 cm with respect to ground level. Detailed descriptions of these habitats are given by Boomsma and de Vries (1980). Similar profiles were determined in a typical Lasius flavus habitat in a stabilized dune grassland at the centre of Schiermonnikoog.

The temperature sensors used were N.T.C. (Negative Temperature Coefficient) thermistors. The resistances were recorded with Grant strip-chart recorders. Calibration values were gathered occasionally by mercury thermometers. Spot readings of the surface temperature were made with an infrared radiation thermometer.

Student's t-test was used for analysis of differences in mean temperature, relative humidity, and global radiation values during flights of the four ant species. If variances were unequal a modified t-test was applied.

Results

Observations on Meteorological Conditions During Nuptial Flights

All observations on flights and meteorological data concerning their commencement are summarized in Table 1 (cf. detailed data in the Appendix). All these flights occurred between 25 July and 1 September. Each year the first *Lasius niger* flight on Schiermonnikoog appeared to be retarded by one or two weeks compared with the first *Lasius niger* flight in the Amsterdam area, which is most probably due to the cooler, more coastal climate of Schiermonnikoog (K.N.M.I. 1972).

It is obvious from Table 1 that the nuptial flights of different ant species do not occur at the same time of day. Lasius niger flights take place in the afternoon shortly after the maximum day temperature, but Lasius flavus flights occur in the late afternoon or early evening. The two Myrmica species have their nuptial flights in the late afternoon, but also in the morning (after 20 August) or even in the early afternoon (Myrmica scabrinodis). Due to these unequal flight times, mean global radiation values are clearly different. Mean global radiation during the flights of Myrmica rubra and Lasius flavus is significantly less (P < 0.001 and P < 0.01 respectively) than during Lasius niger flights (Table 1), if both extensive and local flights are treated as equally important. As a consequence of the positive correla-

tion between the energy and luminosity of radiation fluxes (Kondratyev 1969), the mean light intensity during the flights of these ant species is likewise different. No significant differences could be demonstrated concerning mean flight air temperatures of the different species. Mean relative humidities during flights appeared to be significantly higher for Myrmica rubra than for Lasius niger and Lasius flavus (P < 0.001). Myrmica scabrinodis flights occurred under varying conditions: extensive flights coincided with Myrmica rubra flights, but local flights were observed under much warmer and drier circumstances. For Lasius niger, Lasius flavus, and Myrmica rubra, environmental conditions are the same for extensive and local flights. Wind velocities at 2 m of height never exceeded 1.7 m·s⁻¹ during flights on Schiermonnikoog earlier than 20 August. As wind velocities at Schiphol Airport are higher than the actual wind velocities in town, maximum wind velocities during Lasius niger flights were about equal on Schiermonnikoog and in the Amsterdam area. Later on, especially when no extensive flight has taken place before 20 August, as in 1979, flights may occur at considerably higher wind velocities.

Interruptions of Lasius niger flights were due to clouds (low global radiation), sometimes attended by increasing relative humidity and wind velocity. The only interrupted Lasius flavus flight that could be recorded occurred under conditions of high humidity that are unusual for this species. Rain was never observed during nuptial flights and usually the preceding 12 h were dry as well.

A computer selection of hours which fit to the limitations of Table 1 revealed that nuptial flights indeed took place whenever a suitable combination of meteorological conditions occurred between 25 July and 1 September in 1977, 1978, and 1979. Only four suitable occasions for *Myrmica* flights were selected on which no flights were observed. Although some local flights might have been missed, these exceptions could be easily explained by the very short duration of the suitable period or by the high probability that all alates had already left their colonies in nuptial flights shortly before that occasion. The latter seems the more reasonable, as all these exceptions occurred at the end of the flight season (after 20 August).

It can be concluded, therefore, that the ranges of meteorological parameters from Table 1 are sufficient to cover all possible flight occasions for the four ant species at Schiermonnikoog.

Table 1. Ranges of time, temperature, global radiation, relative humidity, and wind velocity during nuptial flights of Lasius niger, Lasius flavus, Myrmica scabrinodis, and Myrmica rubra. For temperature, global radiation, and relative humidity mean values \pm SE are presented as well; means for extensive flights are given in brackets.

	L. niger	L. flavus	M. scabrinodis	M. rubra	
Time	13.00–17.00	17.00–19.00	12.00-20.00	09.00–12.00 17.00–20.00	
Temperature (°C)	15.9-23.8	18.9–23.1	17.3-23.8	17.3-22.7	
Global radiation (J·cm ⁻² ·h ⁻¹)	133.6-262.9	80.1-168.8	31.3-235.3	31.3-213.0	
Relative humidity (%)	42-70	45–69	43–87	55-87	
Max. wind velocity until 20 August (m·s ⁻¹)	1.7	1.7	1.7	1.7	
Max. wind velocity after 20 August (m·s ⁻¹)	3.4	2.7	2.5	2.5	
Mean temperature ± SE	$19.6 \pm 0.6 (21.2 \pm 1.3)$	20.5 ± 0.6 (20.4 ± 1.0)	20.3 ± 0.8 (18.6 ± 0.6)	19.0 ± 0.6 (18.8 ± 0.6)	
Mean global radiation \pm SE	206.7 ± 10.7 (225.7 ± 19.5)	$138.3 \pm 14.1 (133.2 \pm 20.9)$	161.3 ± 28.6 (104.5 ± 40.1)	97.6 ± 17.9 (110.0 ± 25.8)	
Mean relative humidity \pm SE	57 ± 2 (50 ± 4)	54 ± 4 (55 \pm 5)	61 ± 6 (75 ± 6)	71 ± 4 (72 ± 5)	

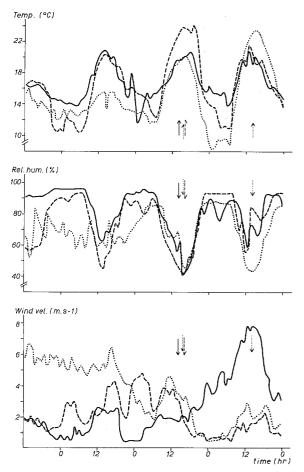


Fig. 1. Flight and preflight patterns of temperature, relative humidity and wind velocity for three extensive *Lasius niger* flights at Schiermonnikoog: 4 August 1977 (solid lines), 20 August 1978 (dashed lines), and 29 August 1979 (dotted lines); starts of nuptial flights are indicated with arrows.

Differences in Flight Conditions for Lasius niger

The queen size in *Lasius niger* is so large that this species needs a period of at least 24 h to enlarge its nest entrances before a nuptial flight can take place. For this reason, a period of two or three days of fine weather is required, especially for the earlier flights of the year.

As summer proceeds, these preflight activities are less intensive, because part of this work was already done before and was not completely destroyed by the rains following. Preflight activities did not occur in *Myrmica* species which have relatively small queens (see also Talbot 1945). For *Lasius flavus*, which lives completely underground, observations concerning preflight activities are not available.

With regard to wind velocities during flights, it is clear from Table 1 that all species and Lasius niger in particular, move their critical thresholds away from 1.7 m·s⁻¹ when time elapses with many sexuals still present in the colonies. In Fig. 1, temperature, relative humidity, and wind velocity during flight and preflight periods are plotted for three extensive Lasius niger flights observed at Schiermonnikoog. Preflight patterns of temperature and relative humidity are rather similar for the flights of 1977 and 1978 and for all extensive flights observed around Amsterdam. However, both preflight conditions and wind velocity during flight were worse for the extensive flight of 29 August 1979. It is interesting that ideal flight conditions were realized only

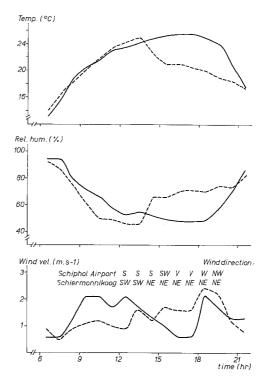


Fig. 2. Temperature, relative humidity, wind velocity, and wind direction for Schiphol Airport (solid lines) and Schiermonnikoog (dashed lines) on 28 July 1978, when an extensive Lasius niger flight took place in Amsterdam at 1500 hours LST and a flight of Lasius niger at Schiermonnikoog was interrupted at 1600 hours LST by incoming sea breeze. For wind direction V means variable.

24 h later, but at that time only local and small scale flights were observed, since most sexuals had left their colonies the day before.

Just after metamorphosis of the sexuals, normally at the end of July at Schiermonnikoog, *Lasius niger* prefers narrower ranges of flight weather conditions. In Fig. 2, temperature, relative humidity, and wind velocity are plotted both for Schiermonnikoog and Schiphol Airport on 28 July 1978. On this day an extensive flight took place in Amsterdam, but a *Lasius niger* flight at Schiermonnikoog was interrupted, apparently because the weather deteriorated at 1400 hours LST. This deterioration was due to an incoming sea breeze, characterized by decreased temperature and increased humidity.

Relationship Between Habitat and Nuptial Flight Conditions

Sand dunes and heathlands, with gradients in height, soil moisture content, and vegetation cover, both contain a number of more or less segregated microhabitats for different ant species (Boomsma and de Vries 1980; Brian 1964). As a consequence of soil moisture content and vegetation cover, each microhabitat also has its own characteristic range of soil temperatures.

Since clear differences in global radiation could be demonstrated for flights of *Lasius niger*, *Lasius flavus*, and *Myrmica rubra*, it seemed interesting to establish the effect of global radiation on soil temperatures in the characteristic ant habitats. In Fig. 3 smoothed temperature curves are given for *Lasius niger* and *Myrmica* habitats on 20 August 1978. Temperatures were recorded at 15 min intervals. Smoothed values were calculated using the formula:

$$\bar{T}_{i} = 0.25 (T_{(i-15)} + 2T_{i} + T_{(i+15)}),$$

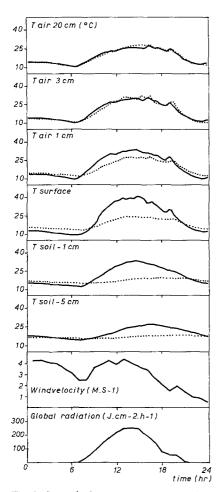


Fig. 3. Smoothed temperature curves (°C) on 20 August 1978 in a Lasius niger (solid lines) and Myrmica habitat (dotted lines). Wind velocities measured at 2 m height, are hourly means. Global radiation values are hourly totals.

where T_i represents the smoothed value for the ith time and $T_{(i-15)}$, T_i , and $T_{(i+15)}$ are measured temperatures, respectively 15 min before, at, and 15 min after the ith time. Fig. 3 shows that there is a clear difference in temperature variation between the habitats of the two species up to 3 cm above ground level. In periods of fine weather, the daily surface and soil temperature ranges in the sparsely-vegetated sand dunes are much greater than in the organic *Festuca* mounds. The grassland soil of the *Lasius flavus* habitat in the older sand dunes shows an intermediate range (see Table 2). It is concluded from these figures that global radiation during nuptial flights is positively correlated with the temperature range in the characteristic habitat of the species concerned. So, the ants that are adapted to the greatest soil temperature ranges fly in periods of high global radiation.

Patterns of daily variation concerning the temperature difference between the nest soil and the air outside were analysed in detail for specific ant habitats. Nest temperatures at depths of between 5 and 7 cm and air temperatures at 20 cm above ground were available for each habitat on two flight days and five similar clear days. The clear days either occurred just outside the nuptial flight period (before 28 July or after 1 September) or were unsuitable for flights due to wind velocities slightly exceeding the thresholds of Table 1. The results are presented in Fig. 4 as smoothed curves of ΔT . ΔT is the difference between the air temperature at 20 cm above ground and the nest temperature at between 5 and 7 cm below ground. ΔT is positive during

Table 2. Maximum, minimum, and range of the daily habitat-temperature curves (°C) for a clear day (for *Lasius niger* and *Myrmica* on 20 August and for *Lasius flavus* on 6 September 1978)

	Maximum			Minimum			Range		
	L.n.	L.f.	<i>M</i> .	<i>L.n.</i>	L, f .	М.	L.n.	L.f.	М.
air 20 cm	28.0	22.6	29.0	10.4	5.0	10.1	17.6	17.6	18.9
air 5 cm	29.8	23.3	34.2	10.4	5.2	7.7	19.4	18.1	26.5
surface	41.0	28.7	24.3	9.0	6.4	13.7	32.0	22.3	10.6
soil-5 cm	27.2	19.8	18.5	14.0	10.6	15.7	13.2	9.2	2.8

∆T(°C)

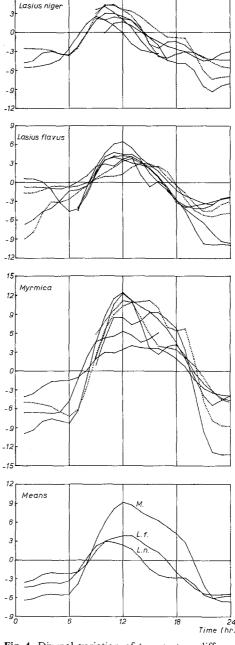


Fig. 4. Diurnal variation of temperature difference ΔT (°C) between air and nest for ant habitats on two nuptial flight days (dotted lines) and five similar clear days (solid lines). Mean ΔT curves for these three habitats are given in the lower figure. The nuptial flight days were: 28 July and 20 August 1978 for Lasius niger and Myrmica and 4 August 1977 plus 12 August 1979 for Lasius flavus.

daytime and negative at night. In all habitats, ΔT changes from negative to positive at about 0800 hours LST. However, the time when ΔT becomes negative is characteristic for each habitat. In the Lasius niger habitat this happens between 1200 hours and 1615 hours LST, for Lasius flavus between 1600 hours and 1800 hours LST, and for Myrmica between 1900 hours and 2030 hours LST. Combination of these data with the flight times presented in the Appendix Table shows clearly that the observed flight times coincide with the times at which ΔT changes from positive to negative for the five successful flights. For the interrupted Lasius niger flight of 28 July 1978 the time when ΔT becomes negative is obviously advanced due to the sudden decrease in air temperature after 1400 hours LST (see Fig. 2). Most other flight times observed for Lasius niger, Lasius flavus, and Myrmica rubra agree with the zero interval of ΔT in the characteristic habitats. Since alate queens, which normally climb in small tussocks or bushes before their actual take off, are aware of air temperatures from this position, we put the hypothesis that queens of Lasius niger, Lasius flavus, and Myrmica rubra prefer to fly at times when the air temperature is about equal to the soil temperature of their nests, provided the ranges of meteorological parameters in Table 1 are met. As Myrmica scabrinodis is distributed over a wider range of habitats than Myrmica rubra, the greater variety in flight conditions of the former species can also be explained by this hypothesis.

Discussion

As a result of the present study, the concept of light intensity and temperature as triggering factors for nuptial flights was both confirmed and refined. The energy content of the light (global radiation) and its effect on soil temperature were introduced as major factors at the beginning of nuptial flights of ant queens. Global radiation primarily affects the soil surface temperature and next the soil temperatures at lower levels (cf. Fig. 3). As far as soil surface temperatures were recorded, these data revealed that the maximum surface temperature at specific flight times in the Lasius niger habitat was 41° C. For Lasius flavus and Myrmica habitats maxima of 33°C and 22°C can be reached during flights. In consequence, the body temperatures of queens, which are on the surface or in the vegetation before takeoff, will be different in the same order as the soil surface temperatures of their habitats at that moment. So, the relatively large and heavy queens of Lasius niger (±25 mg) gain more solar radiation than the slightly smaller queens of Lasius flavus

 $(\pm 18 \text{ mg})$. Obviously, the small *Myrmica* queens $(\pm 4 \text{ mg})$ can ascend at relatively low temperatures of their body. Accordingly, global radiation during flights is also correlated with queen weights of these four ant species.

Since dispersal during nuptial flights is an important process in the maintenance of most ant species, it seems obvious that natural selection will be directed towards survival for queens during and shortly after these flights. Apparently, the avoidance of unfavorable weather conditions can contribute considerably to this goal, but additional preferences for specific flight weather conditions can also be observed in many ant species. Differences concerning time, air temperature, and sometimes relative humidity were demonstrated by Kannowski (1959) and Talbot (1945, 1959) for North American ant species. Kannowski (1969) observed both daily and seasonal periodicities in neotropical army ants. However, reproductive success is achieved only if optimal flight conditions are followed by a proper selection of the most suitable habitat by the fertilized queens. According to the observations of Wilson and Hunt (1966), queens of Lasius neoniger and Solenopsis molesta were perfectly able to select their own macrohabitat during flight. Microhabitat selection occurred after flight by ground search. These results are supported by observations on queens of Lasius niger and Lasius flavus by Pontin (1960).

The similarity between air and soil temperature during nuptial flights could be an important factor in this microhabitat selection by dealated queens, since at the same time soil temperatures in microhabitats of coexisting ant species are different. A similar but less subtle relationship between soil temperature and microhabitat selection was indicated by Brian et al. (1966), suggesting that extremely high soil surface temperatures during flights of *Lasius niger* may prevent queens from settling in the driest parts of southern English heath. Apart from this, references concerning this subject seem to be absent and so the hypothesis – that nuptial flights will not occur if, at specific flight hours, air temperatures are substantially higher or lower than soil temperatures – is considered to be an interesting starting point for analysis of the flights of other ant species.

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Appendix

Species	Date	Time	Place	Quality	T °C	% RH	W m/s	gl·rad·J·cm ⁻² h ⁻¹
L.n.	4 VIII 77	14.00	Sch.	extensive	19.7	56	1.7	262.9
L.n.	19 VIII 77	15.00	Sch.	local	18.7	70	1.5	231.8
L.n.	1 IX 77	17.00	Sch.	interrupted	19.5	67	1.9	146.6
L.n.	28 VII 78	16.00	Sch.	interrupted	21.5	63	2.1	127.4
L.n.	13 VIII 78	15.00	Sch.	local	18.9	58	1.0	222.2
L.n.	20 VIII 78	16.00	Sch.	extensive	23.8	42	1.6	197.0
L.n.	11 VIII 79	15.00	Sch.	local	17.5	55	1.6	171.8
L.n.	12 VIII 79	13.00	Sch.	local	18.8	64	1.3	229.2
L.n.	12 VIII 79	17.00	Sch.	local	19.0	55	1.5	168.8
L.n.	19 VIII 79	15.30	Sch.	interrupted	18.3	79	2.5	120.2
L.n.	25 VIII 79	15.00	Sch.	local	15.9	62	1.3	178.4
L.n.	29 VIII 79	14.00	Sch.	local	19.2	68	3.4	231.9
L.n.	29 VIII 79	15.30	Sch.	extensive	20.1	53	3.2	217.2
L.n.	30 VIII 79	14.00	Sch.	local	23.1	44	1.9	235.3
L.n.	31 VIII 79	17.00	Sch.	local	21.0	55	1.0	133.6

Appendix

Species	Date	Time	Place	Quality	T °C	% RH	W m/s	$gl \cdot rad \cdot J \cdot cm^{-2} h^{-1}$
L.n.	25 VII 78	14.00	N.H.	extensive	20.2	54	1.9	
L.n.	28 VII 78	15.00	A'dam	extensive	25.0	52	1.9	
L.n.	18 VIII 78	15.00	N.H.	extensive	20.6	41	1.9	
L.n.	27 VII 79	14.00	A'dam	extensive	24.3	51	1.1	
L.n.	29 VIII 79	14.00	A'dam	extensive	20.1	53	1.1	
L.f.	4 VIII 77	18.00	Sch.	extensive	20.7	46	1.7	164.1
L.f.	30 VIII 77	18.00	Sch.	extensive	18.9	69	1.1	119.6
L.f.	27 VII 78	19.00	Sch.	interrupted	19.4	87	1.2	114.1
L.f.	20 VIII 78	18.00	Sch.	extensive	23.1	52	0.9	80.1
L.f.	12 VIII 79	17.00	Sch.	extensive	19.0	55	1.5	168.8
L.f.	29 VIII 79	17.00	Sch.	local	20.0	45	2.7	163.3
L.f.	31 VIII 79	17.00	Sch.	local	21.0	55	1.0	133.6
M.	19 VIII 77	15.00	Sch.	local	18.7	76	1.5	231.8
M.	23 VIII 77	11.00	Sch.	local	17.3	81	1.9	189.6
M.r.s.	24 VIII 77	12.00	Sch.	extensive	17.8	59	2.5	213.0
M.	27 VIII 77	12.00	Sch.	local	18.6	72	1.7	210.4
M.r.s.	27 VIII 77	17.00	Sch.	extensive	17.3	72	1.0	31.3
M.r.	30 VIII 77	10.00	Sch.	extensive	17.5	75	2.1	108.2
M.r.s.	27 VII 78	19.00	Sch.	extensive	19.4	87	1.2	114.1
M.r.s.	28 VII 78	20.00	Sch.	extensive	19.7	82	1.7	60.3
M.s.	20 VIII 78	15.45	Sch.	local	23.8	43	0.9	197.0
M.r.	20 VIII 78	20.00	Sch.	local	22.7	65	0.8	57.9
M.r.	21 VIII 78	09.00	Sch.	local	17.6	79	1.0	78.0
M.s.	12 VIII 79	16.00	Sch.	local	19.7	50	1.4	226.6
M.r.	12 VIII 79	18.30	Sch.	local	18.4	61	1.3	81.9
M.s.	30 VIII 79	12.30	Sch.	local	21.9	48	2.5	213.0
M.s.	30 VIII 79	14.00	Sch.	local	23.1	44	1.9	235.3
M.r.	31 VIII 79	17.00	Sch.	extensive	21.0	55	1.0	133.6

List of data concerning nuptial flights of Lasius niger (L.n.), Lasius flavus (L.f.), Myrmica scabrinodis (M.s.) and Myrmica rubra (M.r.) recorded at Schiermonnikoog (Sch.), Amsterdam (A'dam) and the province of North Holland (N.H.); M. indicates that species were not distinguished; times are presented as Local Summer Time (=GMT+2 hours); temperature and relative humidity were recorded at 1.5 m and wind velocity at 2.0 m height. Global radiation values are hourly totals

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