Aphids in nests of *Lasius flavus* F. in Denmark II: Population dynamics

(Aphidoidea, Anoeciidae & Pemphigidae; Hymenoptera, Formicidae)

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Godske, L.: Aphids in nests of *Lasius flavus* F. in Denmark. II: Population dynamics. (Aphidoidea, Anoeciidae & Pemphigidae; Hymenoptera, Formicidae).
Ent. Meddr 60: 21-26. Copenhagen, Denmark, 1992. ISSN 0013-8851.

Quantitative collections of *Lasius flavus* F. and aphids were made during the winter on tidal meadows in Denmark. *Forda formicaria* v. Heyden was found to be the most common aphid, followed by *Forda marginata* Koch and *Geoica utricularia* (Passerini). The total number of aphids per litre varied from 13.96±24.87 to 116.69±122.29. The adult/nymph ratio was recorded. All aphids, which remained in the nests in the wintertime, had an adult/nymph ratio below 30%. Both ants and aphids were aggregated in the upper and southern parts of the nests. The estimated number of *L. flavus* and aphids in a *L. flavus* territory was 46201±25978 ants and 8141±11861 aphids.

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Introduction

Lasius flavus is one of many ant species dependant on the association with aphids. The nature of this association consists of aphid excretion of carbohydrates (honeydew) to the ants in return for protection from parasites and predators. Furthermore the ants also eat the aphids, and thereby regulate the aphid ratio in the nests. Thus the number of aphids in the nests is a key factor in the energenetics of *L. flavus*. Quantitative collections of subterranean aphids in nests of *L. flavus* have been made previously by Muir (1959) and Pontin (1978), but from locations quite different from the tidal meadows investigated in this study. This paper is a continuation of "Aphids in nests of *Lasius flavus* F. in Denmark. I: Faunistic description" (Godske, 1990), in which the aphid species found in association with *L. flavus* on 4 locations in Denmark are described. The aim of this paper is to quantify the distribution of ants and aphids in nests of *L. flavus* from two of the locations, and to describe the population dynamics of the aphid populations in the wintertime. Finally an attempt to estimate the number of ants and subterranean aphids in a *L. flavus* territory on a third location is made.

Localities and methods

The aphid fauna was investigated on three locations: locality No. 1 is a tidal meadow on the island of Alrø, locality No. 2 is a tidal meadow on the island of Samsø and locality No. 3 is a tidal meadow on the peninsula of Skallingen. Soil samples from the nests were taken as soil cores of 7 cm diameter (soilcore area: 38.6 cm^2) and between 16 and 22 cm depth in a pattern shown in fig. 1. Each were divided into an upper and a lower section and the aphids and ants were collected from each sample by extraction in a Berlese funnel. The number of ants, aphid adults and aphid nymphs was counted and the densities per litre were calculated. The aphid species were identified. The adults were distinguished as being the largest individuals of the species, and by being darker and more rounded than the nymphs.

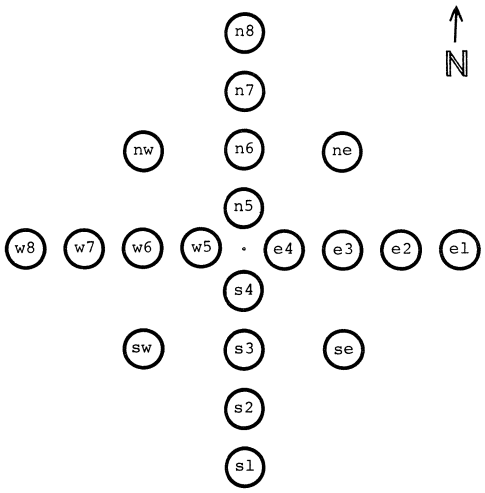

Fig. 1. Distribution of samples in a nest. ne = north-east, nw = north-west, se = south-east and sw = south-east.

The samples from the first two locations were collected in 8 different nests on 6 different dates during the winter 1987-88 and the winter 1988-89. The weather was mild, 8-12°C and cloudy on all sample dates. The sample nests were distributed as follows:

Nest No.	Date	Locality
1	16. Nov. 1988	Samsø
2	16. Nov. 1988	Samsø
3	17. Dec. 1987	Alrø
4	18. Jan. 1989	Samsø
5	19. Jan. 1988	Alrø
6	9. Mar. 1988	Samsø
7	20. Mar. 1989	Samsø
8	20. Mar. 1989	Samsø

Soil samples were collected in June 1989 on locality No. 3 in order to estimate the number of ants and subterranean aphids. Six pairs of nests, with their center about 200 cm apart, were selected in order to estimate the density of aphids and ants in and between the nests. Samples were taken in the nest center and at 20 cm intervals between the centres of each pair of nests. The first two samples were from each nest and the remaining seven were from in between the nests.

Mean height of the 6 pairs of nests involved was 23.8 cm. The territory size for the nests and the zones around the nests was calculated from measurements of the nest-globe in north-south (d1) and east-west (d2) directions and the mean nest height (h). a and b are the radii in the area the nest is covering. When $a = (2 \cdot d1^2) / \pi^2$ and $b = (2 \cdot d2^2) / \pi^2$ the mean area covered by the nests will be $\pi \cdot a \cdot b = 0.63$ m², the mean area of the 0-30 cm zone around the nests

Species	stage	16. Nov. 1988	17. Dec. 1987	18. Jan. 1989	19. Jan. 1988	9. Mar. 1988	20. Mar. 1989	Mean
F. formicaria	adult	1.32	4.74	5.23	7.19	10.06	0.09	4.77
	nymph	7.18	22.79	34.20	41.62	75.46	7.66	32.10
F. marginata	adult	0.39	1.48	2.54	2.28	3.75	2.94	1.90
	nymph	1.35	7.27	7.64	12.99	6.79	0.00	6.66
T. ulmi	adult	0.16	1.00	0.87	0.92	0.00	0.00	0.33
	nymph	1.30	6.59	5.03	3.89	1.76	0.29	2.48
G. utricularia	adult	0.46	1.03	2.83	0.69	2.19	0.16	1.18
	nymph	1.27	3.18	12.64	2.23	7.87	0.64	4.30
G. setulosa	adult	0.18	0.41	2.09	0.00	0.56	0.00	0.01
	nymph	0.36	0.88	6.31	1.77	4.18	0.00	2.25
S. betae	adult	0.08	0.24	0.53	0.27	0.33	0.17	0.13
	nymph	0.57	0.01	1.50	0.27	2.74	1.20	1.34
A. corni	adult	1.16	0.00	0.00	0.00	0.00	0.00	0.30
	nymph	0.31	0.00	0.00	0.00	0.00	0.00	0.08
A. pskovica	adult	0.56	0.00	0.00	0.00	0.00	0.00	0.15
	nymph	0.26	0.00	0.00	0.00	0.00	0.00	0.06
B. pistaciae	adult	0.00	0.18	0.00	0.00	0.00	0.00	0.02
	nymph	0.00	0.76	0.00	0.00	0.00	0.00	0.09
Σ		16.91	50.55	81.41	74.12	116.69	13.69	58.67
N		74	34	30	26	72	52	288

Table 1. The number of aphids (adults and nymphs) per litre, found throughout the winter. Mean = mean number for all sambles. Σ = total of the adults and nymphs of all species on each date. N = number of samples.

will be 1.13 m^2, and the mean area between the nests will be 4.83 m^2.

The mean nest volumen is calculated from $V = area \cdot h / 6 \cdot (3 + h^2 / a^2) = 56.0$ litre.

Results

The following aphid species were represented in the 8 examined nests of *Lasius flavus* at the first two localities: *Forda formicaria* v. Heyden, *Forda marginata* Koch, *Tetraneura ulmi* (Linné), *Geoica utricularia* (Passerini), *Geoica setulosa* (Passerini), *Smynthurodes betae* Westwood, *Baizongia pistaciae* (Linné) (first record in Denmark), *Anoecia pskovica* Mordvilko, and *Anoecia corni* (Fabricius). The number of adults and nymphs of each species is set out in table 1. Collections made on the same date have been pooled.

Table 1 shows that nymphs outnumber adults in almost every case and that the adults/nymph ratio (mean number of adults pr. 1000 cm^3/ mean number of nymphs pr. 1000 cm^3 × 100) varied between the species. The four species *G. setulosa, T. ulmi, F. formicaria* and *S. betae* have an adult/nymph ratio between 11.6% and 18.6%, while *B. pistaciae, G. utricularia* and *F. marginata* have an adult/nymph ratio between 23.7% and 28.6%. *A. corni* and *A. pskovica,* with many more adults than nymphs, have an adult/nymph ratio on 374.2% and 238.9%.

Table 2 ranks species in order of frequency. It shows that *F. formicaria* is the most common aphid in *L. flavus* nests and together with the related *F. marginata* accounts for 77.4% of the number in the samples. Three of the nine species account for 89% of the total number.

F. formicaria	62.8%
F. marginata	14.6%
G. utricularia	9.3%
T. ulmi	4.8%
G. setulosa	3.9%
S. betae	2.5%
A. corni	0.6%
A. pskovica	0.4%
A. pistaciae	0.2%

Table 2. The nine aphid species from nests of *L. flavus* arranged in sequence according to frequency.

Position	No. of ants	S.E.	No. of aphids	S.E.	N
se	647	183	74	25	18
ne	473	178	36	16	18
sw	155	49	44	15	18
nw	392	144	25	16	18
e1	59	20	5	3	14
e2	533	178	50	20	16
e3	502	152	72	24	18
e4	730	189	54	22	16
w5	409	105	72	24	16
w6	460	116	45	18	12
w7	253	75	17	9	12
w8	0	0	0	0	0
s1	153	54	25	14	18
s2	258	75	31	9	18
s3	601	135	64	28	18
s4	732	53	101	30	18
n5	799	174	82	27	16
n6	783	188	66	31	12
n7	352	162	36	16	10
n8	244	225	4	4	2

Table 3. Variation in number of ants and aphids found in different positions in nests of *L. flavus,* expressed as mean number + S.E. per litre.

Table 3 shows the distribution of ants and aphids in the nests as the mean number of every sample-data. Positions as in fig. 1.

The mean number of ants and aphids in the upper and lower part of the divided samples gives a picture of the ants' and aphids' vertical distribution in the nests on each sample-date.

Table 4 shows that in the wintertime both ants and aphids are aggregated in the upper part of the nests. There is a significant difference ($p < 0.05$) in number of aphids between the upper and lower part on all dates, and in number of ants on the last three sample dates. Especially in the collections of 20. Mar. there is a significant difference in the amount of both ahids and ants in the upper and lower parts of the nests ($p < 0.01$).

Date	*L. flavus*		*Aphids*		N
	upper part	lower part	upper part	lower part	
16. Nov.	630	399	22	9	74
17. Dec.	526	309	76	14	34
18. Jan.	630	453	111	32	30
19. Jan.	240	120	100	30	26
9. Mar.	876	444	171	41	72
20. Mar.	425	111	21	1	52
Σ	607	328	82	20	288

Table 4. The distribution of ants and aphids between the upper and lower halves of soil cores taken on each date. N = number of samples in nests.

Results from samples collected in June 1989 in and between nests are shown in table 5.

Table 5 shows that in summer most of the ants stay in the nests, while the aphids aggregate in the nests and just outside the nests. The table also shows the mean number of *L. flavus* and aphids in a *L. flavus* territory to be 46201±25978 ants and 8141±11862 aphids.

Number of ants and aphids in nest

Number	Mean size pr. litre	Mean total of nests	number in nest
Ants	785.1	56.0 litre	43966±23234
Aphids	36.5	56.0 litre	2044±3220

Number of ants and aphids in a 0-30 cm zone from nest

	Number pr. sample	Number pr. m^2	Territory size	Total number in area
Ants	4.2	1090.9	1.13 m^2	1232±875
Aphids	11.8	3064.9	1.13 m^2	3462±3581

Number of ants and aphids between nests

	Number pr. sample	Number pr. m^2	Territory size	Total number in area
Ants	0.8	207.8	4.83 m^2	1004±1869
Aphids	2.1	545.5	4.83 m^2	2632±5081

Table 5. Mean number of ants and aphids in nests, in a 30 cm zone around nest, and between nests ± S.E. Territory size calculations are explained in "localities and methods".

Conclusions and Discussion

Different densities of aphid species in ant nests indicate that they are variously adapted in different ways to the habitat and to the association with the ants.

F. formicaria is the most common aphid in my material, and it is also the only species that is always mentioned in other life studies of *Lasius flavus* (Donisthorpe, 1927; Muir, 1959; Heie, 1973; Pontin, 1978). Zwölfer (1957) found that 80% of a *F. formicaria* population was associated with ants, whereas Sudd (1967) stated that he found the species only in association with ants. Also Muir (1959) found *F. formicaria* to be the most common species in areas with ants; he postulated that the more polyphagous an aphid is, the stronger is its association with ants.

In nests Nos. 1-7 of this study *S. betae* represented less than 10.0% of all aphids,

but in nest No. 8 it represented 22.7% of all aphids. An explanation of the dominance in this nest can be its rich vegetation of dicotyledones (eg. *Artemisia* sp., *Plantago maritima* L., and *Trifolium pratense* L.), since *S. betae* is the only species feeding on dicotyledones.

A. corni and *A. pskovica* are both exclusively holocyclic (they produce sexuales in a annual cycle of generations) and therefore not present in collections made in the wintertime; the specimens found in November probably represent the last individuals of the year's population. This is also reflected in the high adult/nymph ratio in the two species, with a very low production resulting in more adults than nymphs. Pontin (1978) found *A. corni* only from July to November, and he concluded that the species must recolonise the grasses every year (see also Godske, 1990).

All other species have adult/nymph ratios below 30%. The adult/nymph ratio could be the result of a combination of aphid production (fecundity), predation, and migration of alates. Furthermore the possibility exists that there may be specific differences in the adult/nymph ratio in different species.

In the wintertime the solar radiation is most intensive on the southern slope of an ant nest, which means that the overall temperature is higher in this part of the nest. This can explain why both ants and aphids are mainly distributed on the southern side of the nest and in the middle of the nest. Samples taken in the late summer show a dominant distribution on the northern slope (Nielsen et al., 1976). At this time of the year it seems more important for the ants to avoid a drought condition, which can arise in the warmest parts of the nest.

The drainage conditions of the locality can be crucial for the survival of *L. flavus* (Waloff & Blackith, 1962). *L. flavus* can survive submergence for at least 5 days (depending on saltconcentration) (Boomsma, 1982), but it is important that the days with inundation are minimized. Table 4 shows that both aphids and ants aggregate in the upper part of the nest, which generally lies above the water level, and thereby minimize the days with inundation. In the summertime drought is more of a threat for the ants and aphids, and they move downwards in the nest.

Table 5 gives a rough estimate of the mean number of individuals of *L. flavus* and the various aphids in a *L. flavus* territory, based on calculations on territory size and the present data. The calculated number of ants is about twice as large as recorded by Nielsen et al. (1976), and that of aphids is half the number of aphids recorded by Pontin (1978). The wide dispersion of the estimates from their means is probably due to the aggregated nature of the ant distribution (Nielsen et al. 1976), but, of course, the estimations of territory size are only approximations.

Acknowledgements

I thank lektor Mogens Gissel Nielsen, Aarhus University for valuable discussions during my work and for his criticism of the manuscript, and Greg Peakin, School of Biological Science and Environmental Health, London for criticism of the manuscript and for linguistic improvements.

Dansk sammendrag

Bladlus i *Lasius flavus* tuer i Danmark. II: Populationsdynamik.

Kvantitative indsamlinger af rodlevende bladlus og *Lasius flavus* F. blev udført om vinteren på danske strandenge. *Forda formicaria* v. Heyden blev registreret som den mest almindelige bladlus på strandengene efterfulgt af *Forda marginata* Koch og *Geoica utricularia* (Passerini). Det totale antal bladlus pr. liter varierede mellem 13,96±24,87 og 116,69±122,29. Adult/nymfe forholdet blev registreret. Alle bladlus, der forbliver i tuen om vinteren, havde et adult/nymfe forhold på mindre end 30%. Både myrer og

bladlus fandtes først og fremmest i de øverste dele af tuen og i dennes sydlige side.

Beregninger af det totale antal myrer og bladlus i et *L. flavus* territorium giver følgende resultater: *L. flavus:* 46201±25978 individer og bladlus: 8141±11862 individer.

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