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The structure of carrion fly communities: differences in breeding seasons

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A breeding experiment was started in a semi-woodland habitat in mid-August. Only a few adults (45) emerged the same year, but large numbers (over 1000) were collected from the culture pots the following summer. More than half of these were *Sarcophaga scoparia* Pand., a species that was uncommon in experiments started earlier in the season. Three species of Muscidae, which were abundant in an experiment started in June, were now rare or absent. It is therefore suggested that among carrion flies reproductive effort or reproductive success, or both, show seasonal differences which may contribute to local species diversity in this community. These differences are less clear in open habitats, possibly because of the smaller number of species breeding in open (13) than in shaded (20) habitats. Among the flies emerging in individual cultures a negative correlation was found between the numbers of *S. scoparia* and of other species, which supports the above conjectures in showing that competition is probably one factor determining the structure of the community.

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1. Introduction

A breeding experiment on carrion flies conducted in natural conditions in southern Finland in August 1977 (Kuusela & Hanski, in prep.) showed that changes were occurring in the species composition of the local community. At the start of the experiment *Lucilia illustris* (Meig.) was clearly the predominant species, comprising 66 % of the adult female calliphorids (62 % of the calliphorids of both sexes); among the emerging flies the proportion rose to 83 % (82 %) when larval competition was reduced by shortening the exposure period (this reflects the intensity of egg-laying); and finally, in the more natural breeding conditions, when egg-laying was allowed for 1 week and competition among the developing larvae was intense, 91 % (90 %) of the emerging flies were *L. illustris*. We conclude from this that in nature some factors must operate to compensate for the superiority of *L. illustris* observed in this experiment — otherwise *L. illustris* would eventually replace all the other species.

The occurrence of two different kinds of flies, Calliphoridae and Sarcophagidae, in the same pieces of carrion focuses attention on another gap in our knowledge concerning the stability of the species composition. Denno & Cothran (1976) attribute the almost universal coexistence of calliphorids and sarcophagids to a trade-off between dissimilar life history characteristics: sarcophagids are usually larger than calliphorids, and hence probably more powerful fliers (cf. Roff 1977), they have lower fecundity (cf. Zaharova 1966) and slower larval development (e.g. Kamal 1958), but they deposit living larvae, whereas most calliphorids lay eggs and thereby "lose" some time at the start of the utilization of individual corpses (see Hanski & Kuusela 1977 for a theoretical analysis of this "priority effect"). These differences suggest that sarcophagids are better at utilizing small and erratically occurring pieces of carrion. It should be noted that a few other kinds of flies (especially Muscidae) are numerically important in the carrion community, and that in some cases *Necrophorus* beetles are even more important (e.g. Hanski 1976). The former resemble Calliphoridae in life history characteristics.

In the present paper we report a breeding experiment which provides information on the reasons for the numerical stability of species composition, and suggests a unifying explanation.

Our results indicate that the reproductive effort and/or success of the different species varies seasonally, and that *Sarcophaga scoparia* Pand., the predominant sarcophagid in carrion in northern Europe, breeds mainly in late summer. The results of this and previous experiments further suggest that seasonal differences in reproduction are more important in woodlands than in open habitats, where the community is dominated by *Lucilia illustris* (in our study area).

2. Material and methods

The breeding techniques have been fully described elsewhere (Nuorteva 1970, Hanski 1976, Hanski & Kuusela 1977). The experiment was conducted in a small abandoned field (ca. 50 by 100 m) surrounded by woodland, at Lammi Biological Station, southern Finland. The field had been planted with oaks 20 to 25 years earlier, and in 1976 it was, in fact, largely a shaded habitat (canopy ca. 5 m), and supported different types of vegetation in a rich mosaic (the field is known as "Mamre", and was site B in Hanski 1976).

The experiment was started on 13 August 1976, when altogether 80 culture pots were placed at eight different sites in the field, 10 pots at each. These eight sites were at least 15 m from each other. Local soil was used inside the pots, and in each a piece of liver weighing 46.6±6.7 g (*SD*) was provided as food for the maggots. The lids were left open for 24 h to allow egg-laying by calliphorids; afterwards the lids were kept closed but, owing to the design of the pot (Nuorteva 1970), the microclimatic conditions were little distorted from those in the immediate surroundings. During the egg-laying period the maximum daily temperature was 19°C and the minimum 7°C.

The first flies hatched in September 1976, but only a few emerged that year. Collecting was continued until 15 October, when the first snow covered the ground. The culture pots were left intact in their original positions for the winter, and collecting was resumed in early summer 1977 and continued until mid-August, when no further flies were expected to emerge. The pots were checked on 5 and 20 May, 20 June, 3 and 23 July, and 2 and 10 August.

As the pots could not be inspected daily, many of the emerging flies, when collected, were already dead and in poor condition. *Lucilia* spp. could not always be identified to the species. Some of the pots were damaged by frost during the winter, and a few flies managed to escape from these cultures. In addition, seven pots were found to be open at the end of June, and some flies may have escaped from these. These inadequacies of the breeding method may have caused small errors in the results as far as absolute numbers are concerned, but are unlikely to have had any noteworthy effect on the species composition.

Adult flies were trapped from 10 to 15 August 1976 with fly traps of standard type designed by Nuorteva (1959). This was done to ascertain the species composition of the community during the egg-laying period of the present experiment.

3. Results

In mid-August 1976, when the experiment was started, the local calliphorid community was exceptionally rich in species: altogether eight species were recorded, five in large numbers (for comparable experiments see e.g. Nuorteva 1962, 1966, Hanski 1976). Besides the calliphorids, three species of *Sarcophaga* and one carrion-breeding muscid, *Muscina assimilis* (Fall.), were present (Table 1). It is noteworthy that all four species of *Calliphora* were abundant in the same place at the same time. No effort was made to record or identify fly species that do not breed in carrion (for these see e.g. Hanski & Nuorteva 1975, Hanski 1976).

Forty-five specimens, representing eight species, were collected from the culture pots during autumn 1976. The two most abundant species were *Calliphora vicina* Rob.-Des. and *M. assimilis*. No further individuals of *M. assimilis* or *Neoleria inscripta* (Meig.) (Helomyzidae) emerged the following year, but the six other species and four "new" ones were present then (Table 1).

During summer 1977 a total of 1181 individuals emerged, of which 673 (57 %) were *Sarcophaga scoparia* (Table 1). Owing to the infrequent collecting, the seasonal dynamics of emergence could not be assessed (cf. e.g. Hanski 1976), but unexpectedly the clear majority of the flies emerged during the latter half of June (and not earlier). Only one *Calliphora subalpina* (Ringd.) was recorded, but the other three species of *Calliphora* emerged in considerable numbers (Table 1). Because of the bad condition of the material, not all of the 159 specimens of *Lucilia* could be identified. At least *L. caesar* (L.), *L. illustris* and *L. richardsi* Coll. were represented. The last-mentioned was not among the adult flies caught in August 1976, whereas *L. silvarum* (Meig.), which was caught then, was not identified among the flies emerging in 1977 (Table 1). *Hydrotaea dentipes* (Fabr.) and *Scathophaga suilla* (Fabr.) (Scathophagidae) were numerous in the cultures although, for unknown reasons, none were caught in the traps (Table 1).

Table 1 also shows the results of a similar breeding experiment conducted in the same place in 1974, but started in late June (Hanski 1976) instead of in mid-August. Striking differences in the results are apparent: no *S. scoparia* was reared in the earlier experiment, and only one species of *Calliphora* (*vomitoria*) was present, but the three species of Muscidae were much more numerous (Table 1). The numbers of species were 10 (June 1974) and 12 (August 1976); the difference is due

Table 1. Trapping and breeding results in 1976 and 1977. The trapping was carried out from 10 to 15 August 1976. Flies from the cultures were not sexed because of their bad condition. The last column gives the results of another breeding experiment conducted in the same place but started in June 1974 (see Hanski 1976).

	Trapping in 1976			Breeding			
	males	females	%	1976	1977[1]	%	1974[1]
Lucilia illustris (Meig.)	4	5	3		*		180
L. caesar (L.)	7	101	34		*		
L. silvarum (Meig.)		2	1				52
L. richardsi Coll.					*		
Lucilia spp.			38	1	159	13	232
Calliphora loewi Ender.	11	50	19	1	22	2	
C. vicina Rob.-Des.	13	22	11	14	60	6	
C. vomitoria (L.)	9	11	6		54	4	**
C. subalpina (Rigd.)	20	20	13	1	1	1	
Phormia terraenovae Rob.-Des.	2	2	1				
Sarcophaga scoparia Pand.	4	18	7		673	55	
S. carnaria (L.)	2		1				
S. subvicina Rond.	2		1				
Muscina assimilis (Fall.)	6	7	4	17		1	397
Hydrotaea dentipes (Fabr.)				3	26	2	1421
Fannia coracina (Loew.)							31
Scathophaga suilla (Fabr.)				3	186	15	
Neoleria inscripta (Meig.)				5		1	28
Sepsis punctum (Fabr.)							5
Nemopoda cylindrica (Fabr.)							93
Rhyphus punctatus (Fabr.)							11
Total	318			45	1181		2218

* Present

** Present in large numbers (see Hanski 1976)

[1]) The percentage similarity in species composition between these two columns is less than 10.

to the difference in the numbers of culture pots, 15 and 80, respectively (the reason why the total numbers of individuals were higher in the earlier experiment is probably that *H. dentipes* is much smaller than *S. scoparia*, Table 1, Hanski 1976).

In the present experiment, the different species showed dissimilar patterns of distribution over the experimental field (Table 2). For *Sarcophaga scoparia* the variation among the eight sites was not statistically significant ($F = 1.48$; df. 7,72), but for all other species emergence was patchy (Table 2) and, without exception, 50 % or more of the individuals of each species were caught from a single site (21 % in *S. scoparia*). The reason for this difference may well be that *S. scoparia* deposits living larvae, and perhaps only one or a few in one piece of carrion at a time. *Lucilia* females, on the other hand, lay large clusters of eggs, and *Calliphora* females, though usually laying eggs singly, may nevertheless lay large numbers in a single piece of carrion. This difference, which has important ecological and evolutionary consequences, deserves detailed study.

Table 2. Numbers of individuals in different species and at different study sites. Data are expressed as the numbers of culture pots from which the species was recorded/total number of individuals from that site.

	Sites								
	1	2	3	4	5	6	7	8	Total
Lucilia spp.	1/3	3/122	1/15[1]	1/2[2]	2/18[1]				8/160
C. loewi	2/2	1/20			1/1				4/23
C. vicina	1/1		1/13	1/3	3/57				6/74
C. vomitoria						1/3	1/51		2/54
C. subalpina		1/1			1/1				2/2
S. scoparia	5/99	6/62	7/83	6/71	9/140	3/73	5/70	3/32	45/673[3]
M. assimilis		1/12	1/4		1/1				3/17
H. dentipes	1/1				1/13	2/13			4/27
S. suilla	3/93				3/87	1/9			7/189
N. inscripta					2/5				2/5
Total	7/199	7/217	9/115	7/76	10/323	5/98	6/121	3/32	54/1224
No. of species	6	5	4	3	9	4	2	1	10

[1]) All *L. illustris*. [2]) All *L. richardsi*. [3]) One unlabelled sample contained 43 specimens.

Among the emerging flies there was an indication of a negative correlation between the numbers of *S. scoparia* and of the other species, one individual of *S. scoparia* being roughly equivalent to two individuals of other species (Fig. 1), which neatly corresponds to the approximately two-fold difference in their sizes (Denno & Cothran 1976). Two possible explanations would account for the small number of flies collected from many cultures: either few eggs were laid at the start, perhaps because of the relatively short egg-laying period (24 h), or mortality was high because of intense competition, and ultimately because "too many" eggs were laid originally. More importantly, before one can apply any rigorous test of the competition hypothesis, one must make an assumption on the reasons why 26 of the 80 cultures produced no flies at all (Table 2). We observed, after the egg-laying period, that some of the cultures were not infested, but this could not be assessed quantitatively without too much interference. Thus, in the following calculations, which were carried out on the assumption that either 54 or 80 cultures were infested, the latter figure is known to be too high, whilst we cannot be sure that 54 is not an underestimate.

The number of *S. scoparia* were multiplied by 2 to make the counts roughly comparable with those for the other species together (under the present hypothesis). The order in the two sets of counts was then randomized, separately and independently for *S. scoparia* and for the rest of the species. If there is no association or dissociation between the two sets of counts, the results observed (Fig. 1) should agree with the randomized pattern.

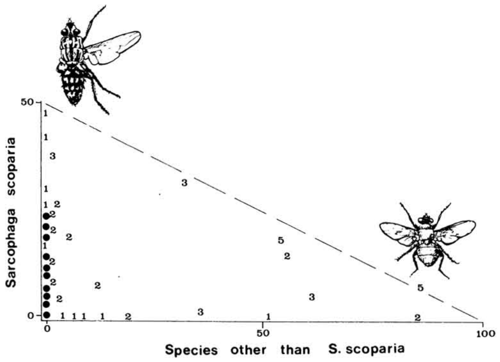

Fig. 1. Numbers of individuals of *Sarcophaga scoparia* and of other species emerging in individual culture pots. Numerals of the graph indicate the number of species in that culture. Overlapping "1"s have been replaced by black dots. The broken line was drawn along maximum combined numbers.

In fact, there was rather good agreement between the observed and randomized distributions, regardless of whether 54 or 80 cultures were used in the calculations (Fig. 2). Nevertheless, only one of the cultures produced over 100 individuals (102, numbers of *S. scoparia* multiplied by 2), whilst the expected number of such cultures was 1.6 (80 pots) and 2.2 (54 pots) (Fig. 2); this difference is not significant, however. One could argue that because we cannot explain why such a large number of cultures produced few or no flies (Fig. 1, Table 2), we should concentrate the analysis on site 5, which produced more flies than any other site, and where there were no "empty" cultures (Table 2). For each culture two numbers were constructed: the number of individuals of *S. scoparia* multiplied by two and the sum of the numbers of individuals of the other species. The smaller of these numbers in each culture was then selected and their sum calculated. The result was 57. The corresponding sum was recalculated 100 times after randomizing the order of the *S. scoparia* numbers. In 11 cases out of 100 a value of less than 57 was obtained, which is certainly compatible with the competition hypothesis, though it does not afford strong statistical support. But whatever the result, the above analysis cannot show that competition did *not* occur, only that competition did or did not (if it occurred) lead to the hypothetized negative relation in the numbers of emerging flies.

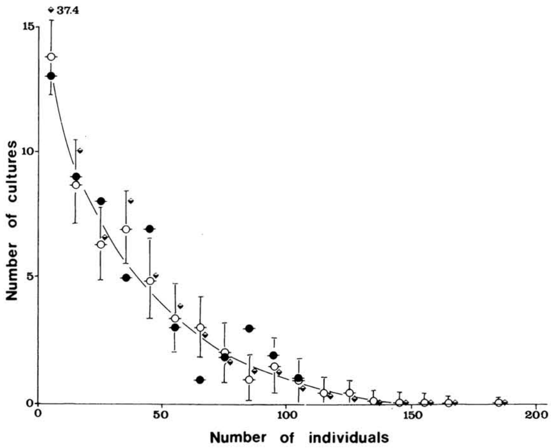

Fig. 2. The distribution of the number of culture pots against the number of flies per pot (grouped in class intervals of 10). The large black dots indicate the distribution observed (see Fig. 1), and the small semi-open dots and the large open circles give the results of the randomization process, explained in the text, for 80 and 54 pots, respectively.

4. Discussion

Various breeding experiments indicate that among the flies emerging from carrion the proportion of sarcophagids is usually small, around 1 % in experiments in southern Finland (Hanski 1976, Hanski & Kuusela 1977), and in U.S.A. (Denno & Cothran 1976), ca 2 % in Japan (Suenaga 1959), and even less in South Africa (Hepburn 1943) and Australia (Fuller 1934). Nevertheless, Fuller (1934) makes the point that in some parts of Australia, where calliphorids are absent or scarce, *Sarcophaga* spp. replace them as the chief carrion-inhabiting flies, but he does not state whether, in the absence of sarcophagids, calliphorids were more abundant than otherwise, as Denno & Cothran (1976) found in their experiments. Hepburn (1943) mentions a higher proportion of sarcophagids in very small pieces of carrion, and similar observations were made by Beaver (1977) on flies bred from snails, by one of us (Hanski) on flies emerging from small (50 g) pieces of carrion in Liberia, West Africa, and by Denno & Cothran (1975) on flies bred from rats, their smallest type of carrion (others were rabbits and sheep). Mihályi (1965), working in Hungary, found that *Sarcophaga scoparia* comprised 17 % of the emerging flies in an experiment covering the whole season, but unfortunately he did not state the size of the bait.

The above observations on the relative abundance of sarcophagids in small pieces of carrion are in agreement with our expectations (Introduction) based on the probable consequences of the differences in life history characteristics between calliphorids and sarcophagids. Nonetheless, it still remains to be demonstrated convincingly that the occurrence of carrion-breeding sarcophagids is dependent on small pieces of carrion. In an experiment with pieces of carrion ranging from 20 to 100 g (a more reasonable range in southern Finland than one from rats to sheep), we failed to find any inverse relation between the proportion of sarcophagids, which were exceedingly scarce, and the size of the carrion (Kuusela & Hanski, in prep.). Instead, the present results strongly imply that, at least in northern Europe, a more important factor may be a seasonally specialized reproduction in *Sarcophaga scoparia*, the predominant sarcophagid.

Fuller (1934) similarly observed that *Sarcophaga hardyi* (J. & T.) and *S. misera* (Walker) visited carrion during the summer (Canberra, Australia), but did not start egg-laying until the autumn; the pupae hibernated, and Fuller explicitly states that the adults emerged late the following summer. These findings were substantiated by laboratory experiments carried out by Zaharova (1971), who found that the onset of pupal diapause in Sarcophagidae is under complex thermal and photoperiodic control. In one experiment, carried out during a cold, rainy summer (average daily temperatures from 14 to 16°C), sarcophagid larvae (4 species) born in June to July turned into pupae which entered diapause (Zaharova 1971). Although in the tropics *Sarcophaga* spp. usually develop continuously throughout the year, exceptionally cold weather may induce pupal diapause in at least some individuals (Denlinger 1978).

Our impression of the seasonal occurrence of *S. scoparia* is at variance with the results of Mihályi (1965), who found that *S. scoparia* females may lay eggs at the beginning of June (in central Hungary). The discrepancy may be explained by the warmer climate in Hungary, and it must be emphasized that even in Finland breeding takes place sporadically throughout the summer (Table 3). Nuorteva (pers. comm.), in his extensive breeding experiments in Finland, has found that *S. scoparia* breeds very erratically, which further complicates the whole problem. In any case, on the basis of the present evidence we suggest that in Finland *S. scoparia* breeds mainly in late summer, and is most abundant in semiwoodland habitats (cf. Tables 1 and 3).

Table 3. Results of three breeding experiments conducted in two open fields at Lammi Biological Station, southern Finland. The 1976 and 1977 experiments were carried out in the same field (see Hanski & Kuusela 1977), which is situated ca. 0.5 km from the second field, where the 1974 experiment was conducted. The number of culture pots was 50 in the first two experiments, and 15 in the 1974 experiment. There were other small differences between the experiments (see Hanski 1976, Hanski & Kuusela 1977), but these do not invalidate the comparison.

	June 1974[1]	August 1976[1]	August 1977[1]
L. caesar		316	806
L. illustris	463	3101	5711
L. silvarum	434	267	312
L. richardsi			38
C. vicina		218	3
C. mortuorum			9
S. scoparia	11	26	8
S. aratrix			2
S. similis	3	5	
S. albiceps		1	
M. assimilis	281	1308	41
H. dentipes		16	9
F. canicularis	171		
Total	1363	5258	6939

[1]) The percentage similarities in species composition are: 60 between June 1974 and August 1976, 39 between June 1974 and August 1977, and 70 between August 1976 and August 1977.

The almost total lack of agreement between the results of the two experiments in Table 1 is unlikely to be due to year-to-year variation alone. Table 3 summarizes the results of three other experiments, also conducted at Lammi Biological Station, but in open habitats, unlike the experiments in Table 1. The experiment started in June 1974 differs most from the others (Table 3), which may be due to either annual, seasonal (June vs. August), or spatial variation (a different site from the two others; Table 3); the interesting point is that differences in species composition between the experiments are much smaller in Table 3 than in Table 1. From this we infer that open and shaded habitats differ in this respect, which would also explain the relatively small seasonal differences reported by Mihályi (1965) and Denno & Cothran (1975). A related phenomenon may be that the number of species per experiment varied less than the total number of species so far reared from the two habitats (20 and 13 from the semi-woodland and the open field, respectively). We do not suggest, however, that the higher species diversity in the woodland site is the cause of the striking seasonal differences in reproduction observed; indeed, the relation may be just the opposite. The present and earlier observations (Fuller 1934, Ullyett 1950, Denno & Cothran 1976) show that competition is probably one factor determining the structure of this community.

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