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SPECIES COMPOSITION, COEXISTENCE AND MORTALITY FACTORS IN A CARRION-EXPLOITING COMMUNITY COMPOSED OF NECROPHAGOUS DIPTERA AND THEIR PARASITOIDS (HYMENOPTERA)

ABSTRACT: In a beech forest on limestone, the community of carrion (dead *Arion ater* slugs) exploiting Diptera and their parasitoids (Hymenoptera) was studied. The carcass sustained 17 species of Diptera and 12 of Hymenoptera. With the exception of *Kleidotoma psiloides* (Eucoilidae), all of the parasitoid species bred were polyphagous and attacked all of the fly species present. The populations of the fly and wasp species were highly aggregated. The degree of aggregation depended in an inversely manner on the density. The dispersion of the parasitoids was independent from the number of hosts. Diptera, which lay their eggs in a late stage of decay, showed a negative correlation between aggregation and the weight of the slugs. There was no interspecific competition detectable between the fly species. The parasitoids did compete markedly only at high levels of parasitism. The parasitoids showed only a weak (negative) density dependent reaction to the number of hosts present. The degree of density dependence was more pronounced in the more infrequent species. The total parasitoid numbers increased in a linear manner with increasing host densities, and therefore the overall parasitism rate was roughly constant for different host numbers. Large predators and necrophages (Silphidae, Carabidae, *Arion ater*) had a high impact on the mortality of the flies and wasps. In experimental boxes that allowed free access to these species, they totally prevented the development of phorid flies and their parasitoids.

KEY WORDS: Hymenoptera, parasitoids, carcass, non-equilibrium systems, competition, density dependence

1. INTRODUCTION

Dead animals are normally a rare resource of patchy distribution and a transient nature. But during decay they often sustain a high number of insect species of three trophic levels (B e a v e r 1977; J o s w i g 1985; H a n s k i 1986; B r a a c k 1987; P e s c h k e et al. 1987): Necrophagous species mostly belong to

the insect orders Coleoptera and Diptera. The next trophic level contains predators (mostly Coleoptera of the families Staphylinidae, Carabidae and Silphidae) and parasitoids (mostly parasitic Hymenoptera and some Staphylinidae). A few hyperparasitic Hymenoptera constitute a third trophic level. Normally, the whole community of species that exploits a certain type of carrion consists of more than 20 species many of which occur only sporadically (Joswig 1985).

Many theoretical considerations have focused on the question of what factors allow such a high number of species to coexist. Today it is generally believed that carrion communities are non-equilibrium systems influenced highly by stochastic events (Caswell 1976; Beaver 1977; Hanski 1982, 1987a, Allen et al. 1993). In these systems coexistence of a large number of species with a high degree of niche-overlap should be possible if the resources are patchily distributed, the species are highly aggregated, and there are refuges of enemy or competition-free space. Therefore, coexistence should be a manner of colonization and extinction of local patches within larger populations (Gurney and Nisbet 1978; Atkinson and Shorrocks 1984; Shorrocks and Rosewell 1986; Hanski 1987a, b; Comins and Hassell 1987). These factors should result in large population fluctuations and high uncertainty in predicting species density. The models of Hassell (1978), Comins and Hassell (1987), Pacala et al. (1990) and Hassell et al. (1991) indicate that density dependent parasitism or predation and higher aggregations of the populations of the superior competitors should promote coexistence as well.

There have been several field and laboratory studies about the population ecology of insects that exploit transient and patchily distributed food substrates. Denno and Cothran (1975, 1976) analyzed the population dynamics of several competing Calliphoridae and Sarcophagidae and found that coexistence may be promoted by the quicker development of the sarcophagid species. According to Beaver (1977) long-term persistence of several species exploiting dead snails is possible because of the heterogeneity of the habitat and the high degree of aggregation of the populations. Kneidel (1984) found only very low degrees of interspecific competition between Diptera breeding in dead snails and in a subsequent laboratory study (Kneidel 1985) he showed that enhancing the degree of patchiness resulted in higher aggregation and lower interspecific competition of the populations. Similar results were obtained by Hanski (1987b). But Reeve et al. (1994) in a study of a salt marsh host-parasitoid system could not detect a sufficient stabilizing effect of aggregation. Concerning the main mortality factors affecting the larvae living in dead animals Peschke et al. (1987), when working with rabbit carcasses, found predation to be very important.

Interestingly, the parasitoids of necrophagous Diptera have been poorly studied. Only Beaver (1977) and Peschke et al. (1987) gave information on parasitism rates and life cycles of the parasitoids. In both studies highly variable parasitism rates (0 to 67%) came up. Studies about density dependence of parasitism and interspecific competition between the parasitoids are obviously lacking.

In the following study I show that dead slugs exposed in a deciduous wood were infested by nearly 20 species of Diptera but that interspecific competition between these species did not effect the

community structure. Desiccation of the carcass, competition with large necrophages, and parasitism seemed to be major mortality factors for the maggots. Total parasitism will be shown to be not density dependent. Finally some hypotheses about ecological differences between necrophagous Diptera and their parasitoids will be developed.

2. MATERIALS AND METHODS

2.1 STUDY SITE

The studies were undertaken in a mixed beech forest (420 m altitude, roughly 120 years old) on limestone near Göttingen (FRG) (see S c h a e f e r 1990 and U l r i c h 1988 for a detailed description of the study area). D i e r s c h k e and S o n g (1982) characterize the vegetation as a Melico-Fagetum subassociation *Lathyrus vernus*. The crown layer is dense and a shrub zone not developed. The herbaceous-flora mostly consists of spring-geophytes that to a great extent disappear in the summer months. Most abundant are *Allium ursinum* and *Mercurialis perennis*.

2.2. EXPERIMENTAL DESIGN

Specimens of all size classes of the slug species *Arion ater* were collected in the Göttingen forest, killed by freezing at −30°C and weighed. In the deposition experiments small (6 × 6 × 6 cm) and large (20 × 20 × 10 cm) boxes of polystyrol were used. The sides of these boxes were made up of fine nylon nets of 0.06 mm (sides and bottom) and 1 mm (lid) mesh wide. This design prevented the dipterous larvae from leaving the boxes to pupate in the soil, but let the necrophages and their parasitoids enter the boxes and allowed even the larger Anthomyiidae, Fanniidae and Panorpidae to deposit their eggs. Large predators and necrophages like Carabids, Silphids and *Arion ater* were kept out. Tests showed that the 0.06 mm mesh width did not hinder the water flux through the bottom of the boxes and, therefore, did not effect the microclimate. Before the first exposure, all boxes were kept in water for one week. This procedure cleared the boxes from all remnants of glue.

To deposit the dead slugs, the bottoms of the experimental boxes were covered with earth, moistened, the slugs covered with beech leaves to prevent the bodies from desiccation, and then exposed (one slug per box).

Two following experiments were performed:

03 August to 01 September 1986

1. 10 slugs from each of 9 size classes: 2–3, 3–4, 4–5...9–10 and 10–12 g weight were placed in 90 small boxes. These boxes were deposited on an area of 1 ha, one box every 10 m.

2. 10 slugs (3–10 g) in 10 boxes without a leave-cover, one box every 10 m.

10 June to 7 July 1987

1. 10 slugs of 3–20 g were placed in 10 large boxes.

2. 10 slugs of 3–20 g were placed in 10 large boxes without a lid. This design let large beetles and other larger species come in but kept out *Arion ater*.

3. 10 slugs of 3–20 g were placed in 10 large boxes without a lid and with open sides. All necrophagous species had access to the dead snails.

After the time of exposure most of the larvae had left the remains of the slugs and pupated. All pupae were sorted according to species, separated and allowed to hatch. Larvae remained in the boxes until they had pupated. They were then sorted. The larvae were moistened from time to time, the pupae were kept dry. To estimate the biomass of the Diptera, I weighed 10 pupae of each species and took the mean values as the species biomass/individual (fresh-weight). Because their pupae were not clearly separable, *Megaselia ?angusta* and *M. ?pulicaria* were treated together.

It is very easy to separate parasitized from not parasitized Phorid pupae. Attacked ones lack the pupal horns that are peculiar to the normal pupae. This difference also makes it possible to detect hyperparasitoids of the pupal stage: species bred out of pupae without horns must have deposited their eggs into pupae with a larval parasitoid already present.

3. RESULTS

3.1. SPECIES USING DEAD SLUGS AND THE COMMUNITY STRUCTURE OF THE DEAD-SLUG ATTACKING FAUNA

A total of 17 dipterous species, of which were 10 Phoridae, and 12 Hymenoptera (mostly Braconidae: Alysiinae, and Diapriidae) emerged out of the dead slugs. Figure 1 and 2 list the most frequent of these species, the stage of decomposition suited for egg deposition of the Diptera, and the parasitoid – host relations. The abundant Alysiinae species *Aspilota* A, B, C and *Orthostigma* sp., and the diapriid *Basalys parva* appeared to be polyphagous with no clear preferences detectable. The eucoilid *Kleidotoma psiloides* was only bred out of *Limosina* sp.

The more infrequent species of Diptera were *Diplonevra florea*, *Triphleba subcompleta*, *Conicera* sp., *Megaselia* sp. (all Phoridae), *Sylvicola ?cincta* (Anisopodidae), *Phaonia ?pallida* (Muscidae), *Psychoda* sp., and two other species of Psychodidae. Additionally bred Hymenoptera were *Atractodes* sp. (Ichneumonidae, out of *Pegomya* sp.(Anthomyiidae)), *Idiotypa nigriceps* (Diapriidae) and *Pentapleura* sp. and 3 species of *Aspilota* (Braconidae, out of frequent Phoridae). 5 species of parasitoids were found in the boxes, but not bred. The pupal parasitoids *Basalys abrupta*, *Trichopria aequata* and *Trichopria evanescens* (all Diapriidae) were found several times, and probably belong to this system too; *Gelis* sp. (Ichneumonidae) and *Ceraphron* sp. (Ceraphronidae) occurred only once. Important large competitors of the dipterous larvae were *Panorpa* sp. (Panorpidae), *Necrophilus subterraneus*, *Necrophorus vespilloides* (Silphidae),

Arion ater

| Conicera schnittmanni | Megaselia ruficornis | Megaselia ?angusta | Megaselia ?pulicaria | Gymnophora arcuata | Limosina sp. | Pegomya sp. |

Conicera schnittmanni
Conicera sp.
Diplonevra florea
Triphleba subcompleta
Megaselia sp.
Sylvicola ?cinctus
Phaonia ?pallida
Fannia ?immutica
Psychoda sp.
Psychodidae sp.
Panorpa sp.
Silphidae spp.
Carabidae spp.
Arion ater

Aspilota D
Aspilota F

Aspilota A
Aspilota B
Aspilota C
Orthostigma sp.

Aspilota A
Aspilota E

Kleidotoma psiloides
Pentapleura sp.

Atractodes sp.

Basalys parva
Idiotypa nigriceps

Basaly parva

Basalys abrupta
Trichopria aequata
Ceraphron sp.
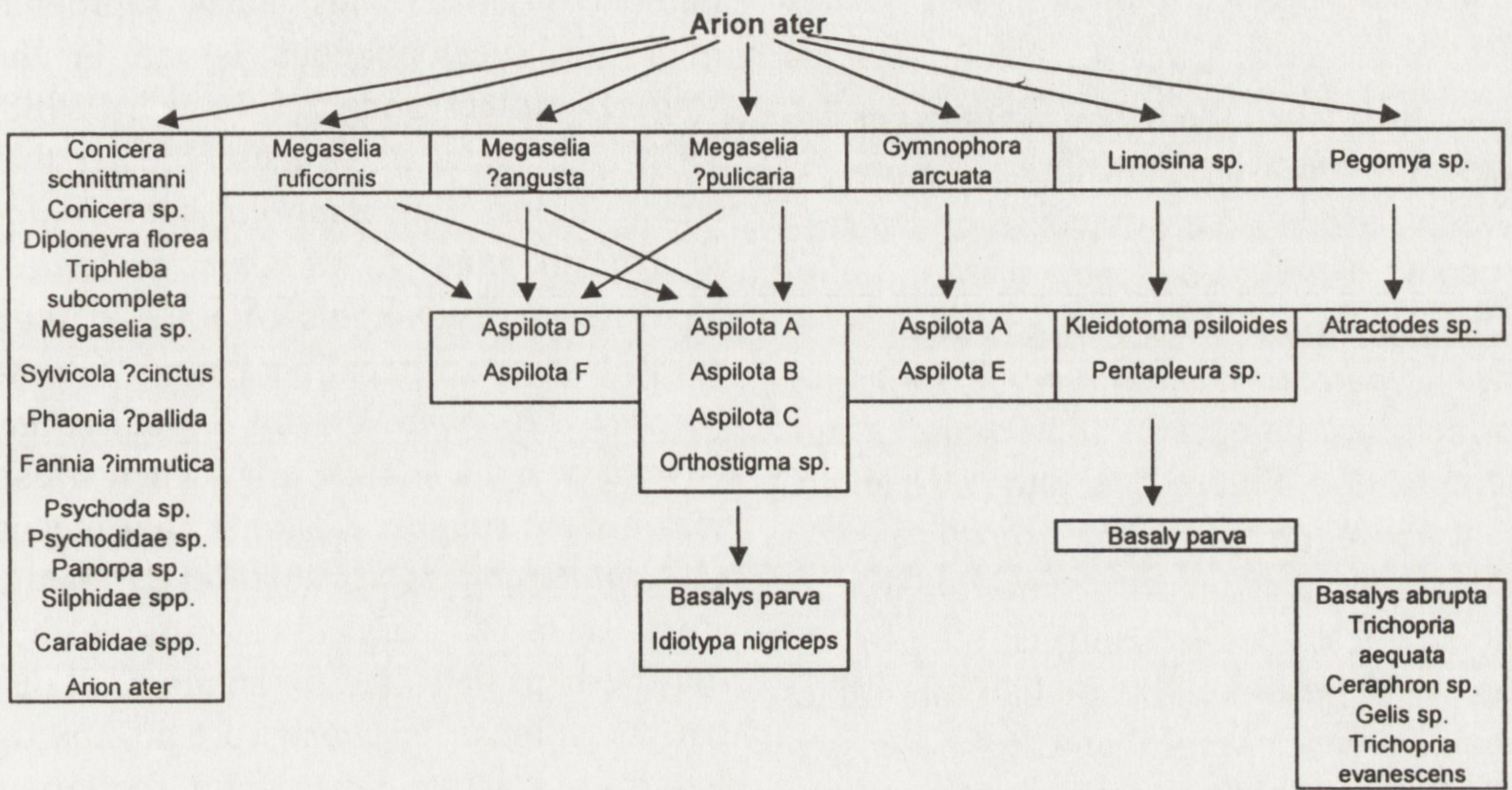Gelis sp.
Trichopria evanescens

Fig. 1. Food web of the species exploiting dead *Arion ater* in the Göttingen forest. The first level contains necrophagous species, the second and third level parasitoids and hyperparasitoids. The parasitoids in the box without arrow were found in the experimental boxes but not bred.

Idiotypa nigriceps
Basalys parva

Aspilota A
Aspilota B
Aspilota D

Aspilota C
Orthostigma sp.

Aspilota A
Aspilota E

Kleidotoma psiloides
Pentapleura sp.

Megaselia ruficornis

M. ?angusta/ ?pulicaria

Arion ater
Necrophilus spp.
Carabus spp.

Gymnophora arcuata

Limosina sp.

Conicera schnittmanni
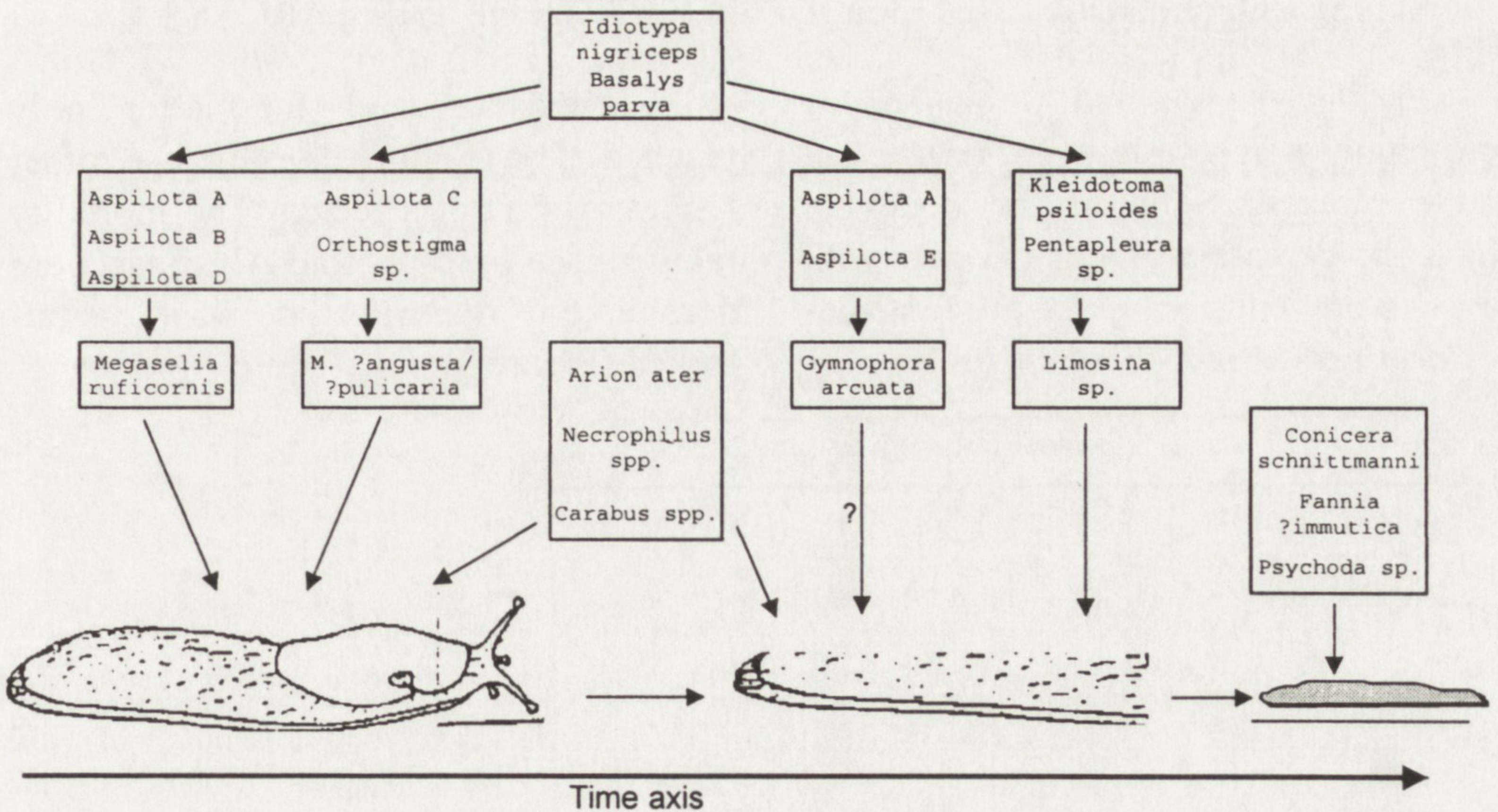Fannia ?immutica
Psychoda sp.

?

Time axis

Fig. 2. Sequence of egg-deposition of the necrophagous species and their parasitoids judged from the sequence of hatching of the species. Due to the low number of individuals, the place of *G. arcuata* is not sure. *B. parva* was not bred out of *G. arcuata*, but probably also attacks this species. It is also shown at which stadium of decay other necrophages feed on the dead snails. The upper level are hyperparasitoids, the next level is made up of parasitoids, the next lower levels are necrophages.

Carabus spp. (Carabidae), and *Arion ater*.

Only 6 of the 17 Diptera were attacked by parasitoids (Table 5, Figure 1). This was neither an outcome of the frequency of the species nor of the time of egg deposition: the most abundant species, *Conicera schnittmanni* (Table 1) (which lays its eggs in a late stage of decomposition, Figure 2) and the also abundant *Psychoda* sp. (which deposits early), did not serve as hosts. *C. schnittmanni* is the smallest species using the slugs (0.3 mg pupal fresh-weight and half this value imaginal fresh-weight) and *Psychoda* sp., together with *Limosina* sp., are the next smallest (0.6 mg pupal fresh-weight). In the Göttingen beech forest some quite large ichneumonids, many Alysiinae, 2 eucoilids, nearly all diapriids and a number of chalcidoids attack saprophagous or mycetophagous larvae in the soil/leaf litter zone (U l r i c h 1988, 1998). The smallest of these species that attack larvae (an *Aspilota* sp., *Pentapleura* sp. and *Kleidotoma psiloides*) have mean dry-weights of 0.02 to 0.03 mg; the smallest pupal parasitoids (*Basalys parva*, *B. cymocles* and *B. pedisequa*) have a weight ~ 0.01 mg. Their fresh weights are roughly 10-fold. That means *C. schnittmanni* is too small even for the smallest larval parasitoids present, but may perhaps be suited for some small pupal parasitoids. *Psychoda* sp. and *Limosina* sp. are at the lower limit for larval parasitoids. Indeed, the smallest larval parasitoids, *K. psiloides* and *Pentapleura* sp. as well as the small pupal parasitoid *B. parva*, were bred out of *Limosina*.

3.2. FACTORS THAT EFFECT THE DEVELOPMENT OF THE NECROPHAGOUS DIPTERA, DESICCATION OF THE CARCASS

C. schnittmanni and *M. ruficornis* were highly susceptible to the drying out of the carcasses. Out of the boxes in which the carcass was not covered with leaves to prevent drying out, the first species declined to less than 1% of the normal abundance and the latter only reached 5% (Figure 3). But the other Diptera were not affected. The mortality rates caused by parasitoid Alysiinae were normal, but *Limosina* sp. was less attacked (Figure 3).
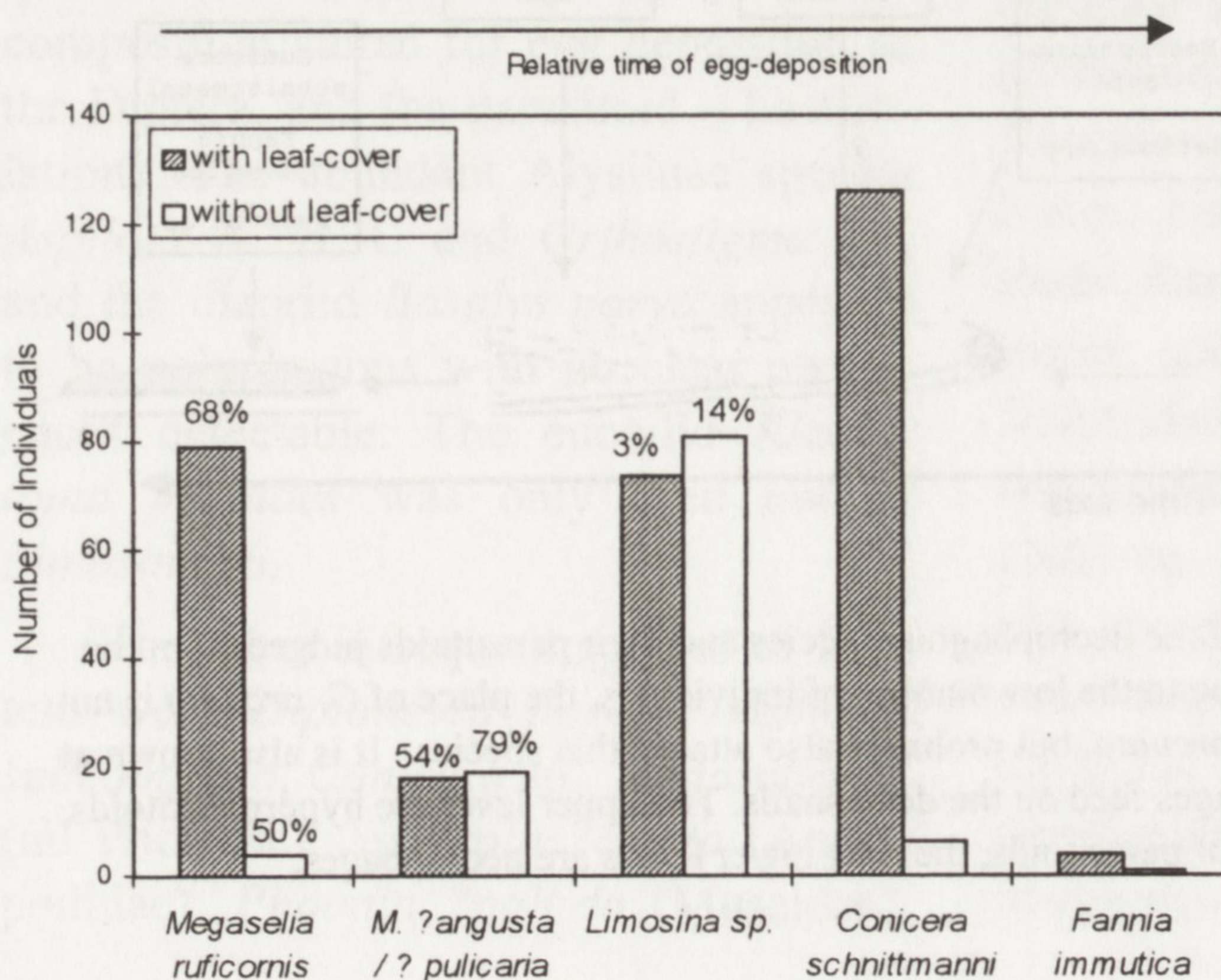

Fig. 3. Reaction of the necrophagous Diptera on the desiccation of their feeding substrate. Results of breeding experiments (number of individuals bred) in which the dead snails were covered with leafs or remained uncovered. The uncovered snails dried out very fast. Given is also the percentage of parasitism.

3.2.1. Biomass of the slugs

As expected, the number of individuals and the total biomass of most of the species was positively correlated with the weight of the slugs (Tables 1 and 2), but all of the r-values are surprisingly low (< 0.6) and only those of *C. schnittmanni*, *M. ?angusta/?pulicaria*, *Psychoda* sp., and *Limosina* sp. were statistically significant (p < 0.01). Only 34% of the variance of the total weight of all flies bred per slug is explained by the biomass of the slugs (correlation coefficient: r = 0.59). The results of a multiple regression (with the numbers of all fly species and the slug weight as dependent variables and based on the breeding of all 90 exposed slugs) showed that for *C. schnittmanni* the weight of the slug explained

only 14% of the total variance and for *Limosina* only 10%. All other species were not significantly affected by the biomass of the slugs. That means small slugs were as well suited for development as large ones. This result is also supported by the ratio of slug weight to the total biomass of the dipterous pupae: the mean freshweight of the slugs was 6.54 g which resulted in a dry weight of 0.59 g. The highest combined fresh weight of all pupae which developed in one slug reached only 0.3 g. On average the total biomass of the pupae was 0.069 g fresh weight per slug. Therefore, a maximum of only 50% (but probably not more than 10%) of the body mass of the dead snails could have been consumed by the flies.

3.2.2. Interspecific competition

If the species compete with each other there should be a negative correlation between the number of larvae of one species against the larval-number of the other species that develop in a dead snail. But no such mutual exclusion or even reduction between the fly species could be detected (Table 2 and 3). Only three of the multiple R-values are statistically significant, and these depend solely on the positive correlation with the weight of the slugs. Significant negative correlation between species did not occur, but *Li-*

mosina sp. and *M. ?angusta/?pulicaria* correlated even slightly positive (R = 0.23, Table 2). Additionally, in the case of *C. schnittmanni* the predicators explained only 32% of the total variance, and of course in all of the non-significant runs there was no variance explanation. That means the occurrence of all of the species was not detectable affected by the presence of others. The data give no hint of any interspecific competition between these necrophagous Diptera.

3.2.3. Effect of large competitors and predators

The presence of large competitors and predators (Carabidae, Silphidae, *Arion ater*) had a high impact on the developmental success of the Diptera (Figure 4). Out of boxes without lids, *Megaselia ?angusta/?pulicaria, Gymnophora arcuata* and *Limosina* sp., which

deposit their eggs in the middle stage of decay, hatched in a drastically reduced number. The more early depositing *M. ruficornis* also reached a lower density; however this was statistically not significant. On the other hand, the larger *Diplonevra florea* and another larger

Table 1. Total number of Diptera and Mecoptera bred out of 9 weight classes of *Arion ater*. Also listed are the rank correlations (Spearman's rank, r(S)) between the number of necrophages and the mean fresh-weight of the snails. Significant r-values (p < 0.01) are marked with °.

Weight class of the snails [g]	No. of							
	Conicera schnittmanni	*Megaselia ruficornis*	*Megaselia ?angusta / ?pulicaria*	*Psychoda* sp.	*Panorpa* sp.	*Limosina* sp.	*Fannia immutica*	*Gymnophora arcuata*
2–3	20	67	7	2	4	28	1	3
3–4	126	79	18	6	3	74	4	0
4–5	181	94	44	15	4	75	9	1
5–6	151	67	62	32	2	179	0	9
6–7	519	55	15	21	6	123	20	4
7–8	315	104	1	37	3	181	1	26
8–9	713	101	109	39	1	285	12	2
9–10	861	48	90	63	3	321	21	6
10–12	1118	75	159	54	2	413	0	2
r(S)	0.97°	−0.21	0.63	0.97°	0.48	0.98°	0.14	0.27

Table 2. Correlation and partial correlation between the fresh weight (mg) of the important Diptera and Mecoptera developing in dead *Arion ater*. Upper part (above the dashes): simple correlation between the species. Lower part (below the dashes): partial correlation with the elimination of the weight of the dead snails. ° – p < 0.01. The correlations were done with all 90 experimental boxes.

Species	*Conicera schnittmanni*	*Megaselia ruficornis*	*M. ?angusta / ?pulicaria*	*Gymnophora arcuata*	*Limosina* sp.	*Psychoda* sp.	*Fannia immutica*	*Panorpa* sp.
Conicera schnittmanni	–	−0.19	0.17	−0.15	0.14	0.14	0.18	0.09
Megaselia ruficornis	−0.15	–	−0.03	0.09	−0.11	−0.03	0.17	−0.02
M. ?angusta / ?pulicaria	0.32°	−0.03	–	−0.13	0.23	0.02	−0.02	0.09
Gymnophora arcuata	−0.04	0.08	−0.09	–	−0.13	−0.05	0.1	−0.07
Limosina sp.	0.38°	−0.1	0.37°	−0.06	–	0.21°	−0.13	0.05
Psychoda sp.	0.01	−0.03	−0.08	−0.08	0.11	–	−0.07	−0.11
Fannia immutica	0.2	−0.16	0.01	0.11	−0.07	−0.04	–	0.13
Panorpa sp.	0.04	−0.02	0.06	−0.07	0.01	−0.13	0.12	–
Weight of *Arion ater*	0.55°	−0.002	0.35°	0.11	0.51°	0.25°	0.09	−0.07

Table 3. Results of a regression analysis to detect a possible reduction of the biomass of necrophagous Diptera and Mecoptera by the presence of other species.

Species	Multiple r	R^2	p	ß-weight of the snails	p	ß-weight of necrophages	p
Conicera schnittmanni	0.562	0.316	<0.001	0.493	<0.001	0.130	0.189
Megaselia ruficornis	0.189	0.036	0.206	0.139	0.293	–0.236	0.076
M. ?angusta / ?pulicaria	0.390	0.152	0.001	0.218	0.077	0.220	0.074
Gymnophora arcuata	0.187	0.035	0.212	0.221	0.096	–0.193	0.146
Limosina sp.	0.523	0.274	<0.001	0.437	<0.001	0.135	0.221
Psychoda sp.	0.261	0.068	0.046	0.298	0.020	–0.075	0.559
Fannia immutica	0.138	0.019	0.432	0.004	0.979	0.136	0.315
Panorpa sp.	0.130	0.017	0.479	–0.164	0.250	0.150	0.297

The biomass of each species listed was tested against the sum of the biomasses of all other species and against the biomass of the snails.
The analysis was run over the 90 experimental boxes of all snail weights.
ß-weight refers to the standardized coefficient of the multiple regression.
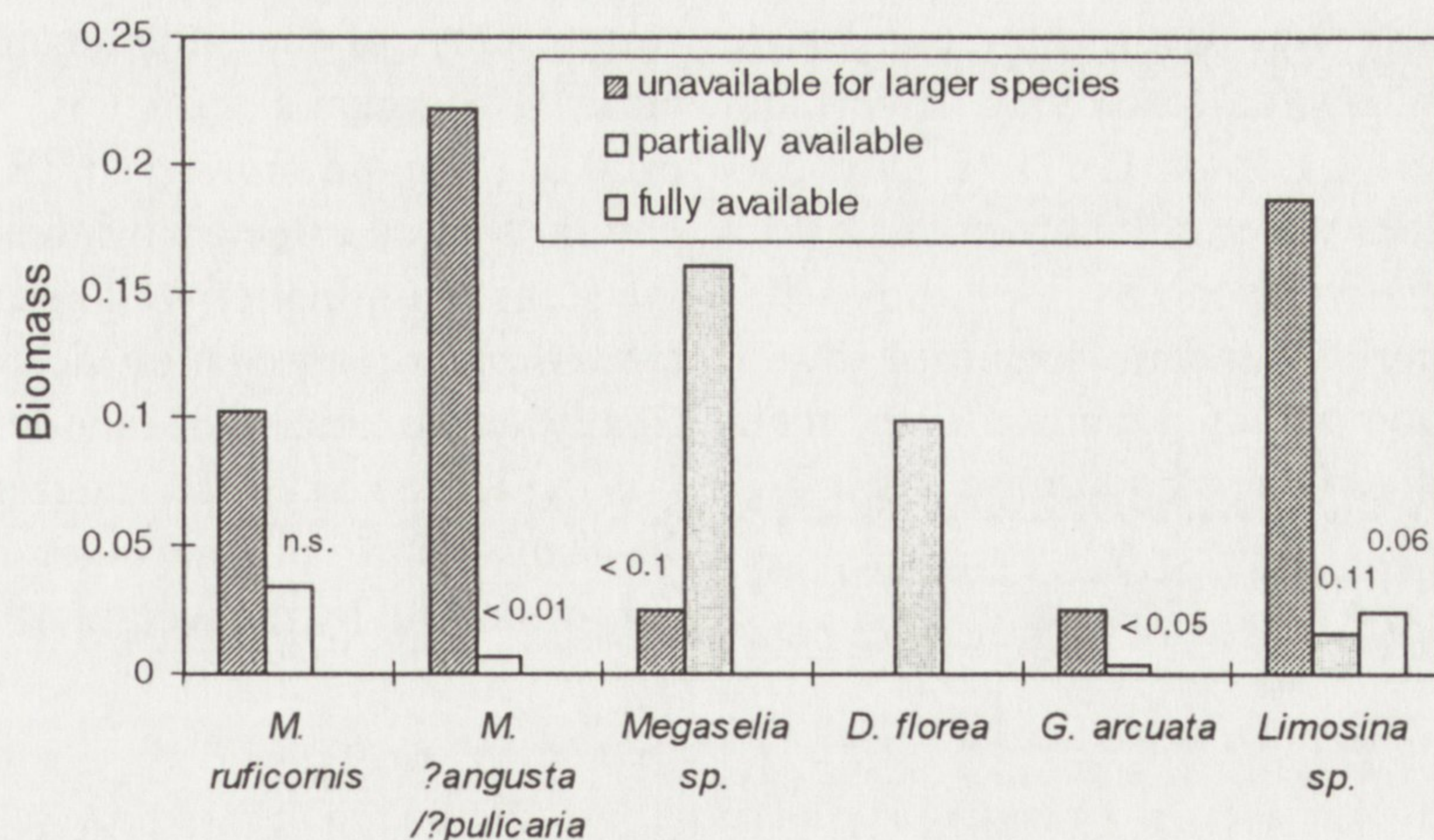

Fig. 4. Reaction of the Diptera feeding on dead *Arion ater* on the presence of larger competitors. Biomass: Total dry weight of each species bred. Given are also the levels of significance p(t). Partially available: to boxes without lid larger Diptera had access; fully available: to boxes without a lid and with open sides all necrophages (including Coleoptera and *Arion ater*) had access.

species of *Megaselia* reached higher abundances. Out of the boxes that allowed all the possible consumers access to the dead snails, only a few individuals of *Limosina* sp. emerged. No other species was found. These results point to the fact that the access of other competitors or predators has a high impact on the structure of the fly-community. The smaller *Megaselia* spp. are excluded, but larger species reach higher densities. Less affected are species which deposit in a late stage of decay. But the difference in abundance of the fly species can-

Table 4. Correlation (Spearman's rank) between the biomasses of necrophagous flies bred
out of experimental boxes that allowed large competitors access to the dead snails

Species	Spearman's r	p(t)
Megaselia ruficornis – Megaselia sp.	0.67	0.05
Megaselia ruficornis – Diplonevra florea	–0.19	n.s.
Megaselia ?angusta / ?pulicaria – Megaselia sp.	0.42	n.s.
Megaselia ?angusta / ?pulicaria – Diplonevra florea	0.23	n.s.
Limosina sp. *– Megaselia* sp.	0.32	n.s.
Limosina sp. *– Diplonevra florea*	0.42	n.s.

not simply be interpreted as a competition due to food shortage. (Table 4). Five out of six correlations between the biomass of the fly species are positive. That means both small and large fly species do not exclude each other but rather inhabit suitable substrates together.

3.2.4. Aggregation

All fly species occurred in an aggregated manner (as measured by the Lloyd-Index, L l o y d 1967) (Figure 5, 6). The values were in the order of 1.5 to 9 and normally reached values above 2, and the more abundant species had a lower degree of aggregation than the more infrequent ones (r = 0.87, p < 0.05).

The dispersion of *C. schnittmanni* (correlation of degree of aggregation per weight class of the slugs against weight class, Spearman's rank: $R_S = -0.90$, p< 0.001) and *Limosina* sp. ($R_S = -0.52$, p = 0.15) was affected by the weight of the slugs: with higher weight class of the carcasses the aggregation decreased and finally approximated a random distribution (Figure 5). The aggregation of *Megaselia* spp., on the other hand, was not influenced by the weight of the slugs.

3.3. PARASITISM OF THE NECROPHAGOUS DIPTERA

3.3.1. Parasitism rates

The larval parasitoids caused high parasitism rates in the Phoridae and Sphaeroceridae (Table 5). 80.7% of the maggots of *M. ruficornis* were attacked, 54.3% of *Megaselia ?angusta/ ?pulicaria*, 36% of *G. arcuata* and 13.8% of *Limosina* sp. Pupal parasitoids were only infrequently bred. They and the hyperparasitoids reached no more than 0.2% parasitism.

The weight of the slugs had no influence on the parasitism rates of the dominant parasitoid species (Kruskal-Wallis test between the weight classes of the slugs: p > 0.3). Flies in small slugs suffered the same parasitism as flies in large ones. But the recedent *Aspilota* C reached slightly higher parasitism rates in larger carcasses (Spearman's rank correlation between parasitism rate and weight of the
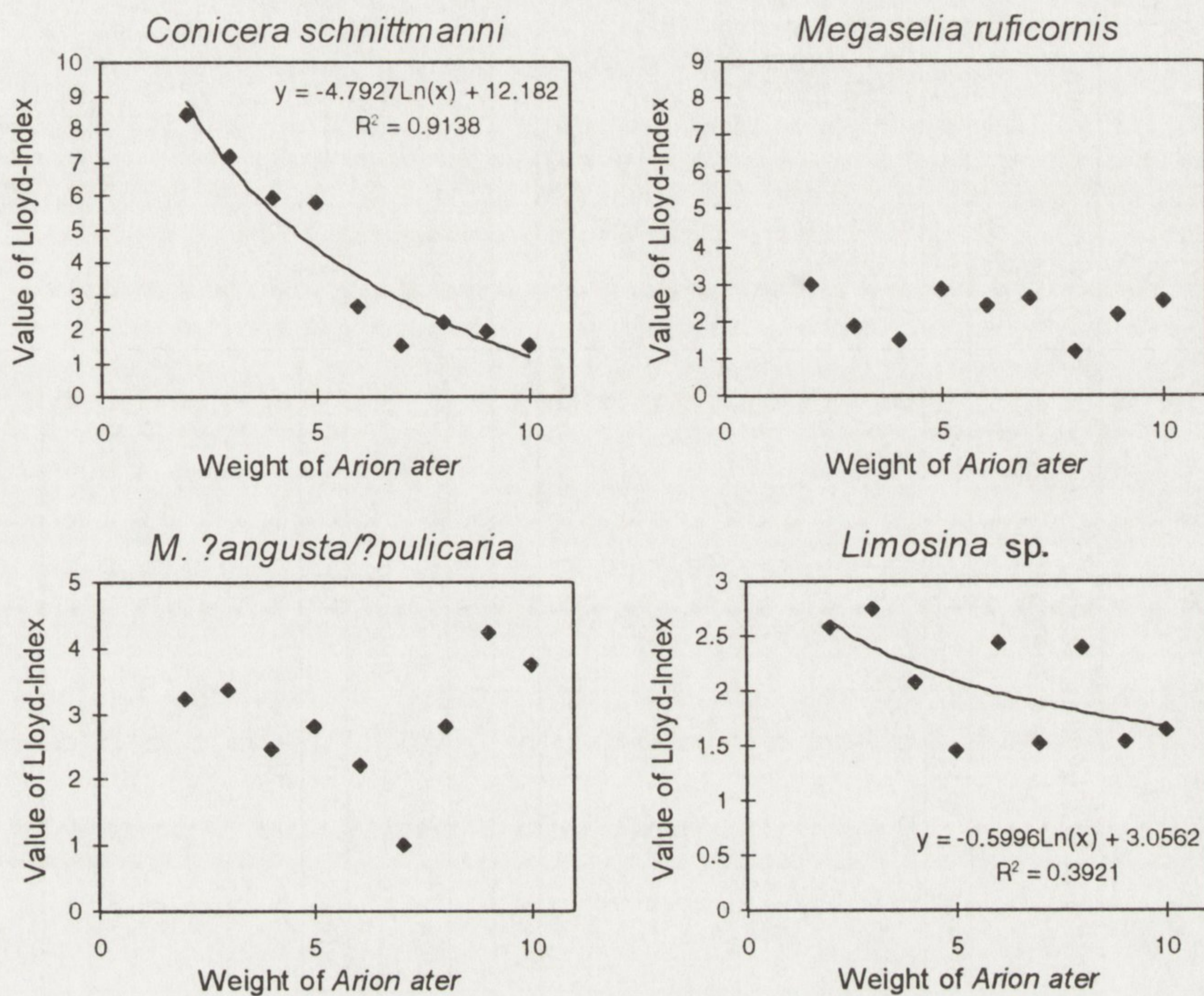
Figure 5. Level of aggregation of the dominant necrophagous species versus weight-class of the dead snails. The Lloyd-index was computed using the 10 experimental boxes of each weight-class.

slug: $R_S = 0.29$, $p < 0.01$). Thus, most parasitoids did not discriminate between the size of the substrate, and small patches were as intensively searched for hosts as large ones.

3.3.2. Aggregation

All of the parasitoids were highly aggregated (Figure 6). But there was no clear linear correlation between rank order and aggregation as was the case for the hosts. Of course, the value of the Lloyd-index depends in part on the degree of aggregation of the host populations. Therefore, in the case of the more abundant species the values are higher than the host values.

The dispersal pattern of each of the species was neither correlated with the parasitism rate nor with the number of hosts or the weight of the substrate (no significant correlation at a 5% level). Therefore, the different values of the Lloyd-index should reflect real differences between the species.

3.3.3. Density dependence of parasitism

Due to the high variance in parasitism at low host densities (Figure 7, 8) it is difficult to assess the type of dependence between the numbers of parasitoids and hosts. To detect a possible dependence I computed least square linear regressions between parasitoid and host densities of four types: arithmetic linear, logarithmic, power, and exponential (Table 6). Zero counts were included by X+1

Table 5. Mean number of necrophages N, their fresh-weight W (mg), and the parasitism rates in the experiment with *Arion ater*. % Par.: mean parasitism rate.

August 1986			*Aspilota* A	*Aspilota* B	*Aspilota* C	*Aspilota* D	*Aspilota* E	*Aspilota* F	*Ortho-stigma* sp.	*Basalys parva*	*Kleido-toma psiloides*	Sum
Host	N	W	% Par.	% Par.	% Par.	% Par.	% Par.	% Par.	% Par.	% Par.	% Par.	% Par.
Conicera schnittmanni	44.5	28	0	0	0	0	0	0	0	0	0	0
Megaselia ruficornis	7.7	8	30.1	14.6	5.5	0.3	0	1	29.1	0.1	0	80.7
M. ?angusta / ?pulicaria	5.6	6	13.5	36.0	1.5	1.6	0	0	1.5	0.2	0	54.3
Gymnophora arcuata	0.6	1	35.8	0	0	0	0.2	0	0	0	0	36.0
Limosina sp.	18.7	11	0	0	0	0	0	0	0	0	13.8	13.8
Psychoda sp.	3.0	3	0	0	0	0	0	0	0	0	0	0
Fannia immutica	0.8	3	0	0	0	0	0	0	0	0	0	0
Panorpa sp.	0.3	7	0	0	0	0	0	0	0	0	0	0
Others	0.1	1	0	0	0	0	0	0	0	0	0	0
Sum	81.3	68										

June 1987			*Aspilota* A	*Aspilota* B	*Aspilota* C	*Penta-pleura* sp.	*Atrac-todes* sp.	*Basalys parva*	*Idiotypa nigriceps*	Sum
Host	N	W	% Par.	% Par.	% Par.	% Par.	% Par.	% Par.	% Par.	% Par.
Megaselia ruficornis	9.3	10.0	0	1	0.9	0	0	0.1	0	1.9
M. ?angusta / ?pulicaria	20.1	20.0	7.5	11.9	4.9	0	0	0	0.1	24.3
Gymnophora arcuata	0.8	1.3	13.5	0	4.8	0	0	0	0	18.3
Limosina sp.	33.7	20.0	0	0	0	0.2	0	0	0	0.2
Pegomya sp.	0.3	20.0	0	0	0	0	67	0	0	67.0
Others	7.8	80.0	0	0	0	0	0	0	0	0
Sum	72.0	151.3								

or Y+1 transformations. At values of slope B well above 1 high R^2-values in logarithmic regressions point to inverse density dependence, high R^2-values in regressions of the power or exponential type point to direct density dependence. This reverses at slope-values (B) below 1. Good arithmetic linear regressions, low values of R^2, or slope values (B) around 1 allow no rejection of the null-hypothesis of density independence.

The total parasitism of the Alysiine species was clearly density independent (Table 6, Figure 8). The arithmetic linear regression gave the best result and the slopes of the other regressions are all near the value of 1. Of course, the slope of the arithmetic linear regression (B = 0.73) reflects the mean parasitism rate of the *Megaselia* spp.

However, if one looks at the different species, no clear pattern occurs. Most likely, the parasitism of the three more abundant species, *K. psiloides* and *Aspilota* A and B, is density independent. Arithmetic linear regression gave the best results and in the other regression types no conclusive trend occurs. But in the case of the less abundant *Orthostigma* sp. and *Aspilota* C parasitism seems to be inversely density dependent. In both species the exponential type (with slopes well below 1) and the logarithmic type (with slopes well above 1) gave the best fits. But the high variance in parasitism and the resulting low degree of variance explanation (R^2) allows no definite conclusion.
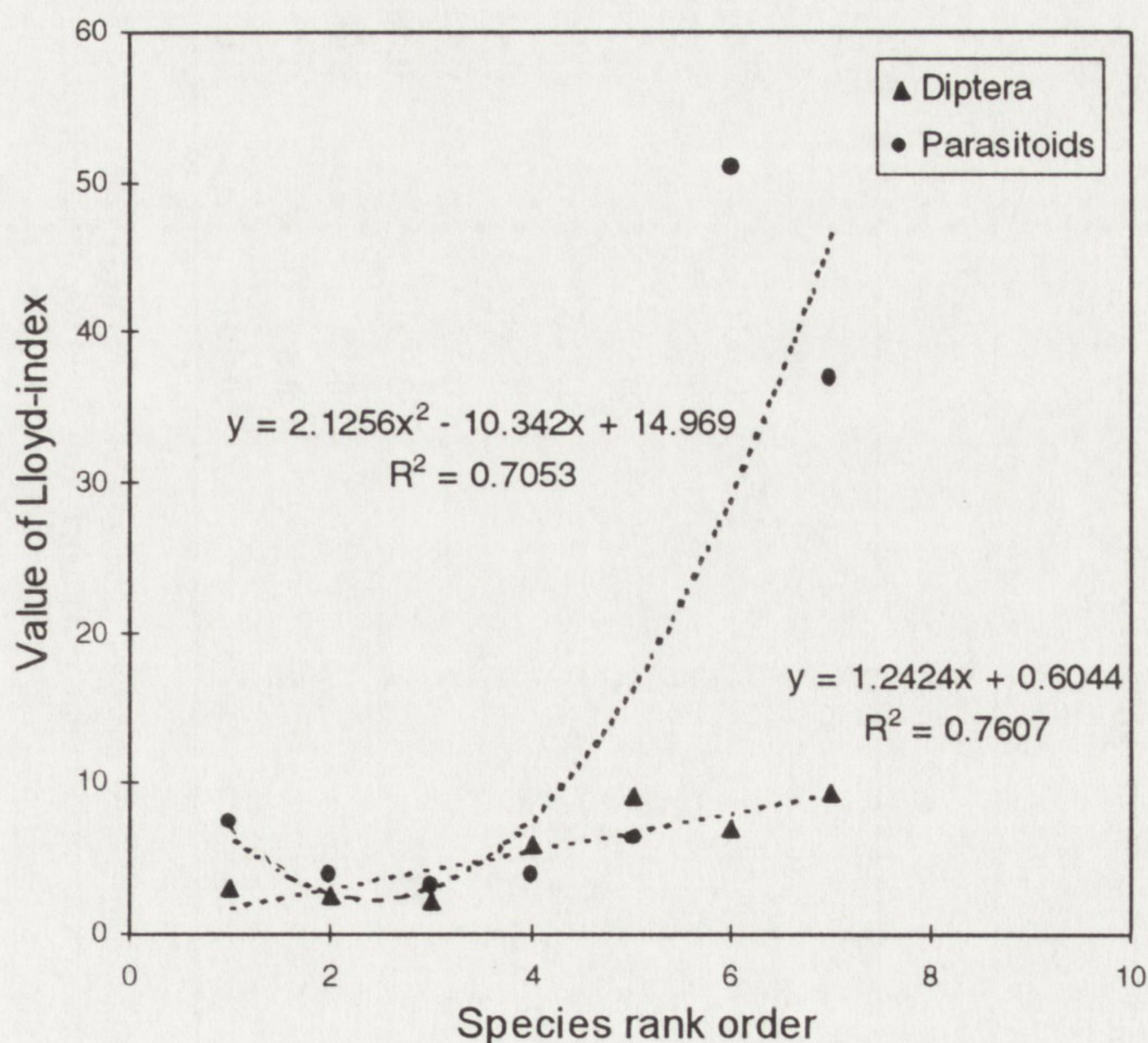

Fig. 6. Aggregation and species rank order (abundance of the species). The value of Lloyd-index was calculated over all 90 experimental boxes with dead *Arion ater*.

Table 6. Results of a regression analysis with the number of parasitoids (X) as the dependent and the number of hosts (Y) as the independent variable.

Type of equation used	Parameters	*K. psiloides*	*Orthostigma* sp.	*Aspilota* A	*Aspilota* B	*Aspilota* C	All Alysiinae
Logarithmic	B	1.45	1.75	1.40	1.25	16.1	1.11
	R	0.59	0.39	0.51	0.51	0.25	0.79
	P	<0.001	<0.001	<0.001	<0.001	0.02	<0.001
Power	B	1.02	1.01	1.03	1.04	1.01	1.05
	R	0.58	0.30	0.50	0.66	0.22	0.74
	P	<0.001	<0.001	<0.001	<0.001	0.03	<0.001
Exponential	B	0.58	**0.43**	0.56	0.60	**0.15**	0.99
	R	0.59	**0.43**	0.53	0.56	**0.27**	0.85
	P	<0.001	**<0.001**	<0.001	<0.001	**0.02**	<0.001
Arithmetic linear	B	**0.12**	0.08	**0.21**	**0.41**	0.02	**0.73**
	R	**0.62**	0.27	**0.58**	**0.75**	0.23	**0.94**
	P	**<0.001**	0.02	**<0.001**	**<0.001**	0.03	**0.001**

In the case of logarithmic transformed variables values of (X+1) and (Y+1) were used to include zero counts.
B: slope of the regression, R: coefficient of correlation, P: two tailed significance level.
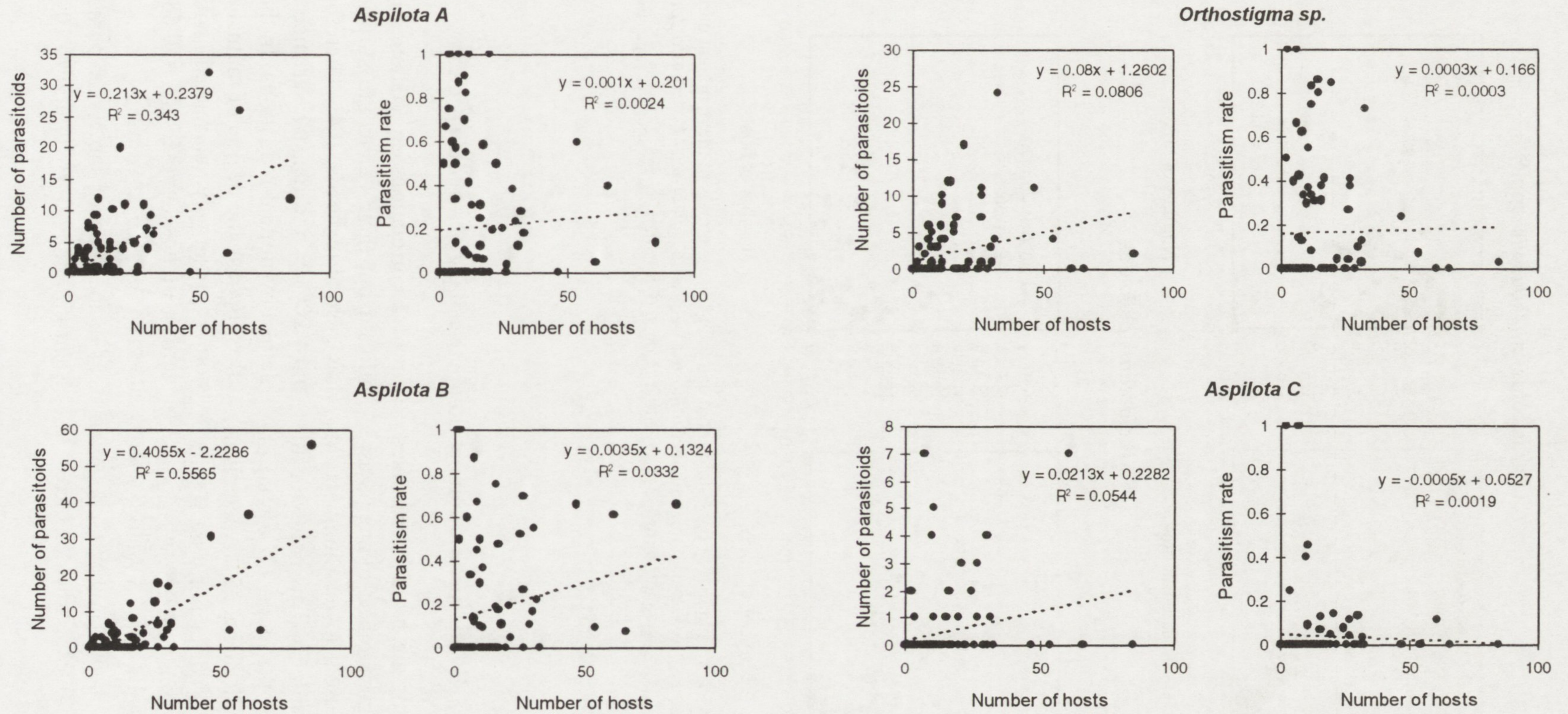Best regressions are given in bold font.

Fig. 7. Dependence of the number of parasitoids bred and the parasitism rates of the dominant parasitoid species on the number of hosts (*Megaselia ruficornis* and *M. ?angusta /?pulicaria*) feeding in dead *Arion ater*.

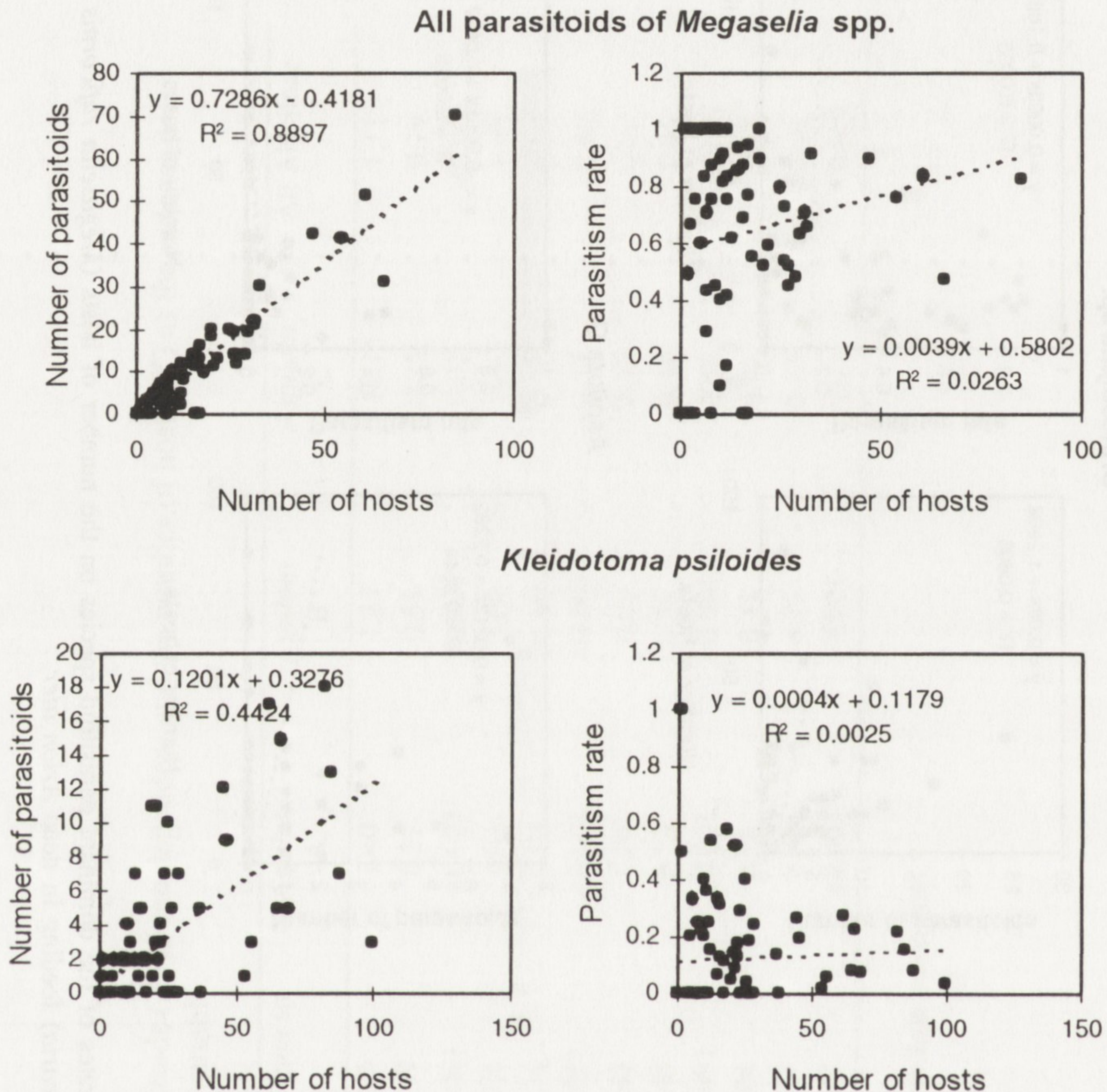### All parasitoids of *Megaselia* spp.

Fig. 8. Dependence of the number of parasitoids bred and the parasitism rates of the dominant parasitoid species (Alysiinae and *K. psiloides*) on the number of hosts (*Megaselia ruficornis*, *M. ?angusta/?pulicaria* and *Limosina* sp.) feeding in dead *Arion ater*.

3.3.4. Interspecific competition between the parasitoid species

In the case of the higher parasitized *M. ruficornis*, high numbers of one parasitoid species caused lower numbers in other species (Table 7). This holds for all weight classes of the slugs. Of a total of 38 correlation coefficients 35 are negative. However, only 10 correlations are significant at the 5% level (at the 5% significance level 2 significant correlations are expected just by chance). When computed over all of the 90 experimental boxes 3 out of 4 correlations are statistically significant but their values are surprisingly low. None exceeds 0.4. Therefore, at most 20% of the density variance is explained by mutual reductions. In the case of *Aspilota* A the degree of mutual exclusion is positively correlated with the number of hosts present (r = 0.68; p < 0.05).

In the case of the lesser parasitized *Megaselia ?angusta/ ?pulicaria* 10 out of

25 correlation coefficients are negative (this deviates not significantly from the null-hypothesis of equal chance between positive and negative values) (Table 8).

These results support the view that interspecific competition between the parasitoid species of this community is low.

Table 7. Competition between the parasitoids of *M. ruficornis*. Correlations between the parasitism rates of one species against the sum of the parasititism rates of the other species bred.
Significant correlation ($p < 0.05$) are marked with °.

Weight class of the snails [g]	Number of *M. ruficornis*	*Aspilota* A / others	*Aspilota* B / others	*Aspilota* C / others	*Orthostigma* sp./ others
2	67	–0.570°	–0.33	–0.51	–0.47
3	79	–0.4	–0.28	–	–0.28
4	94	–0.66°	–0.48	–0.22	–0.57°
5	67	–0.18	–0.15	0.21	–0.07
6	55	–0.13	–0.07	0.48	–0.09
7	104	–0.44	–0.3	–	–0.3
8	101	–0.99°	–0.91°	–0.67°	–0.89°
9	48	–0.26	–0.33	–0.28	–0.25
10	75	–0.12	–0.24	0.5	–0.03
Sum	690	–0.37°	–0.25°	–0.16	–0.31°

Table 8.Competition between the parasitoids of *Megaselia ?angusta / ?pulicaria*. Correlation between the parasitism rates of one species against the sum of the parasitism rates of the other species bred.
Significant correlations ($p < 0.05$) are marked with °.

Weight class of the snails [g]	*M. ?angusta / ?pulicaria*	*Aspilota* A / others	*Aspilota* B / others	*Aspilota* C / others	*Orthostigma* sp./ others
2	23	–	–	–	–
3	29	–0.15	–0.15	–	–
4	107	0.16	0.32	–	0.65°
5	92	0.65°	0.84°	0.51	–
6	36	–	–0.06	–0.06	–
7	13	–	–	–	–
8	134	–0.27	–0.24	–	0.22
9	167	0.05	0.23	0.5	–0.13
10	190	0.13	–0.1	0.4	0.41
Sum	791	–0.03	–0.05	0.1	0.15

4. DISCUSSION

Ephemeral substrates, such as dung or carrion, have been the object of many theoretical publications (H a n s k i 1981, 1985; A t k i n s o n and S h o r r o c k s 1981, 1984; H a s s e l l et al. 1985; H a s s e l l 1986; G r e e n 1986; S h o r r o c k s and R o s e w e l l 1986; C o m i n s and H a s s e l l 1987). Their models of persistence of the food webs and coexistence of the species expect:
– a high aggregation of the species,
– a patchy distribution of the resources,
– a more pronounced aggregation in the superior competitors,
– density dependent parasitism patterns.
Were these predictions met ?
In studies comparable to the present one B e a v e r (1977) found 18 species of Diptera infesting the snail *Cepaea nemoralis* (Helicidae) and K n e i d e l (1984) reported 15 dipteran species bred out of dead slugs. H a n s k i and K u u s e l a (1980), when using liver as substrates, found 13 species of Diptera in an open and 20 species in a shaded habitat. The species number reported here (17) agrees with these findings.

As predicted all species occurred in a highly aggregated manner. This result is in accordance with previous studies on insects inhabiting slug carcasses (B e a v e r 1977 and literature therein). But, in contrast to theoretical predictions (A t k i n s o n and S h o r r o c k s 1981, 1984), the infrequent species of both, hosts and parasitoids, tended to be more patchily distributed than the more abundant ones (Figure 6). In this context it is very interesting that the only parasitoid species without competitors, *K. psiloides*, was the least aggregated.

For *C. schnittmanni* and *Limosina* sp. the degree of clumping was dependent on the weight of the slug. Probably, these late arriving species were more affected by the suitability of the carrion than early ones: with regard to the probability of drying out or otherwise becoming unsuited, small patches differed more than large ones. Hence large carcasses could be exploited more equally.

High total parasitism rates of the species were correlated with lower degrees of clumping (taken all the individuals bred into account) (Figure 9). This behavior is best explained if one assumes that all species visit the breeding sites randomly and lay a roughly constant, species specific number of eggs. This behavior would lead to independently aggregated dispersions with a declining degree of crowding when higher densities are reached (G r e e n 1986).

Of course, the substrates were patchily distributed, but the data do not allow conclusions to be drawn as to whether this fact enhances the coexistence of several species (as the theoretical considerations suggest). Previous studies showed no conclusive results. In laboratory studies with carcass-patches K n e i d e l (1984, 1985) found a lesser degree of interspecific competition between necrophagous Fannidae and Phoridae but this did not prevent competitive exclusion. On the other hand H a n s k i (1987a, b) was able to achieve a long-term coexistence of fly species through an experimentally increased patchiness.

Interspecific competition between the necrophagous Diptera turned out to be very low. Similar conclusions were drawn by K n e i d e l (1984). In a laboratory study (K n e i d e l 1985) he showed that at least 64 eggs each of two dipteran species per gram slug were necessary for strong competition between the two spe-
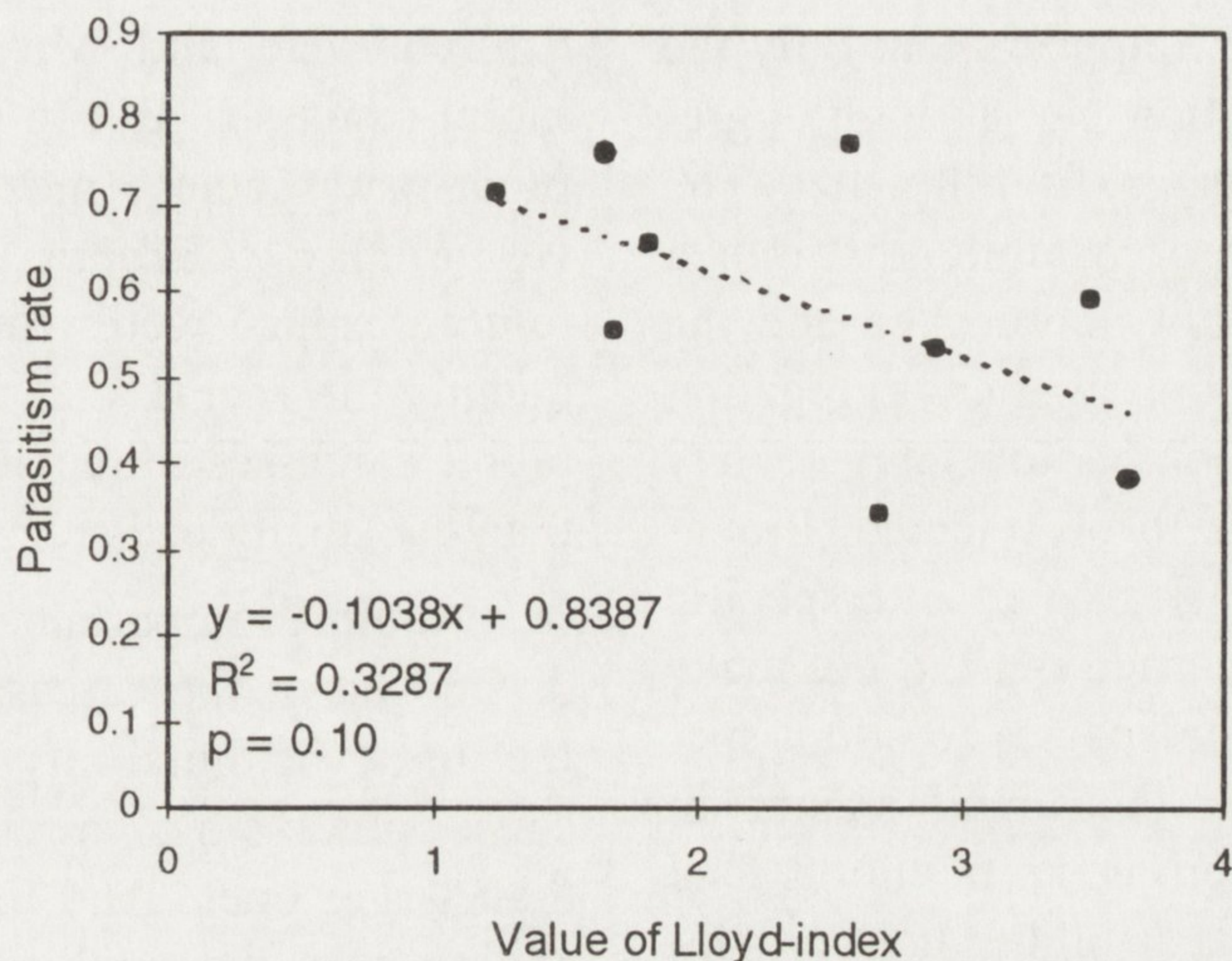
Fig. 9. Parasitism rates and values of Lloyd-index of the Alysiinae bred out of dead snails. The 9 data points are the mean values in the 9 weight-classes of *A. ater*.

cies. In the experiments reported here a mean of only 13 larvae per g slug occurred. In the best case there were 44 larvae per g slug. Even if one takes a low egg mortality and possible negative effects under natural conditions into account, the resulting value will lie well below the threshold for strong competition.

Concerning the main mortality factors affecting the Diptera it appeared that large competitors / predators (the experiments allowed no definite distinction between these two groups) and parasitoids were of major importance. Drying reduced the numbers in some species but left others unaffected. The data given in Figure 3 and 4 indicate that Diptera that deposit in an early stage of decay suffer more from parasitoids (*M. ruficornis*) and that later arriving species are more reduced by desiccation of the carcass and competitors/predators.

The more abundant parasitoid species showed no density dependent parasitism pattern. A slight tendency to inverse density dependence characterizes the less frequent species. Positive density dependence did not occur. Total parasitism was clearly not density dependent. Dempster (1983), Lessels (1985) and Stiling (1987) compiled publications about parasitoid host interactions and also found a rather low percentage of density dependent parasitism patterning. Dempster could detect in only 3 out of 24 lepidopteran life tables a density dependent regulation by predators/parasitoids. Lessels and Stiling found percentages of 35% (17 out of 49 cases) and 25% (43 out of 171 cases), respectively. An inverse density dependent pattern occurred in 30% and 23% of cases, respectively. This means that in more than 50% of the reported case studies parasitism was density independent. The computations of Stiling revealed that density independent parasitism is frequent when the hosts are Diptera and free-living and the parasitoids are solitary and endoparasitic. These are the conditions especially met by the parasitoids of the necrophagous flies in the present study.

In summary, it appears that only the theoretical prediction No. 1 (high aggregation of the species) is fully met. The stabilizing effect of patchily distributed substrates could not be checked and the other two predictions (higher aggregation of the superior competitors and density dependence) have to be rejected. Probably the very low degree of interspecific competition that turned out did not make it necessary for the species to adopt special strategies for their maintenance in this carrion exploiting community. One can speculate that, at higher host or substrate densities, the high degree of aggregation, perhaps in combination with the high mortality rate suffered due to larger predators, is sufficient to sustain this community. When the interspecific competition is higher, the number of species decreases and species with additional strategies become superior.

The low degree of interspecific competition between the fly species does not mean that competition has no long-term effects. But other influencing factors are clearly more important in organizing the community and affecting the densities. First of all, the competition between the flies and larger necrophagous species, such as Silphids, Carabids and *Arion*, should be considered. The most frequent saprophagous competitors found in or near the boxes were *Panorpa* sp. (Mecoptera), *Necrophilus subterraneus* (Silphidae) and *Arion ater*. The fact that no Phoridae emerged out of the boxes that allowed all of these users access showed that they are important competitors and mortality factors for the flies.

The impact of predation may depend on the type of the carcass. P e s c h k e et al. (1987) found that predatory Silphidae and Staphylinidae were the most important mortality factors for necrophagous

Calliphoridae and Muscidae inhabiting rabbit carcasses. But in the present study predatory species (mostly *Necrophorus vespilloides*, *Carabus* spp. and *Philonthus* spp.) were found only infrequently. It seems that the much larger rabbit carcasses attracted more predators than the small dead slugs.

Another important factor was the drying-out of the carcasses. This may in fact limit the suitability of the slugs, because small slugs are more susceptible than larger ones. And this fact may also explain why the smallest slugs contained fewer larvae of late-arriving species (*C. schnittmanni*, *Limosina* sp.) and that these species were more highly aggregated.

The fourth main factor is the mortality caused by parasitoids. This should have a high influence on the structure of the fly community, because of the very different parasitism patterns. The *Megaselia* species turned out to be highly parasitized (on average 73%), while the others were mostly unaffected.

The higher degree of competition between the parasitoids should lower the diversity. This is indeed the case (Figure 10). The Shannon-diversity is 1.8 for the necrophagous Mecoptera and Diptera and only 1.3 for the Parasitoids, the evenness for the Hymenoptera is also lower (0.64, but 0.81 for the fly species). If the diversity is measured by the slope of the species abundance-rank order, the flies have an index of -0.39 and the parasitoids one of -0.79. Both species rank relationships follow linear regressions.

Table 9 lists the main differences and similarities between the necrophagous and the parasitoid community that turned up in this study. Both groups contain a high number of species; these are patchily distributed, and the interspecific
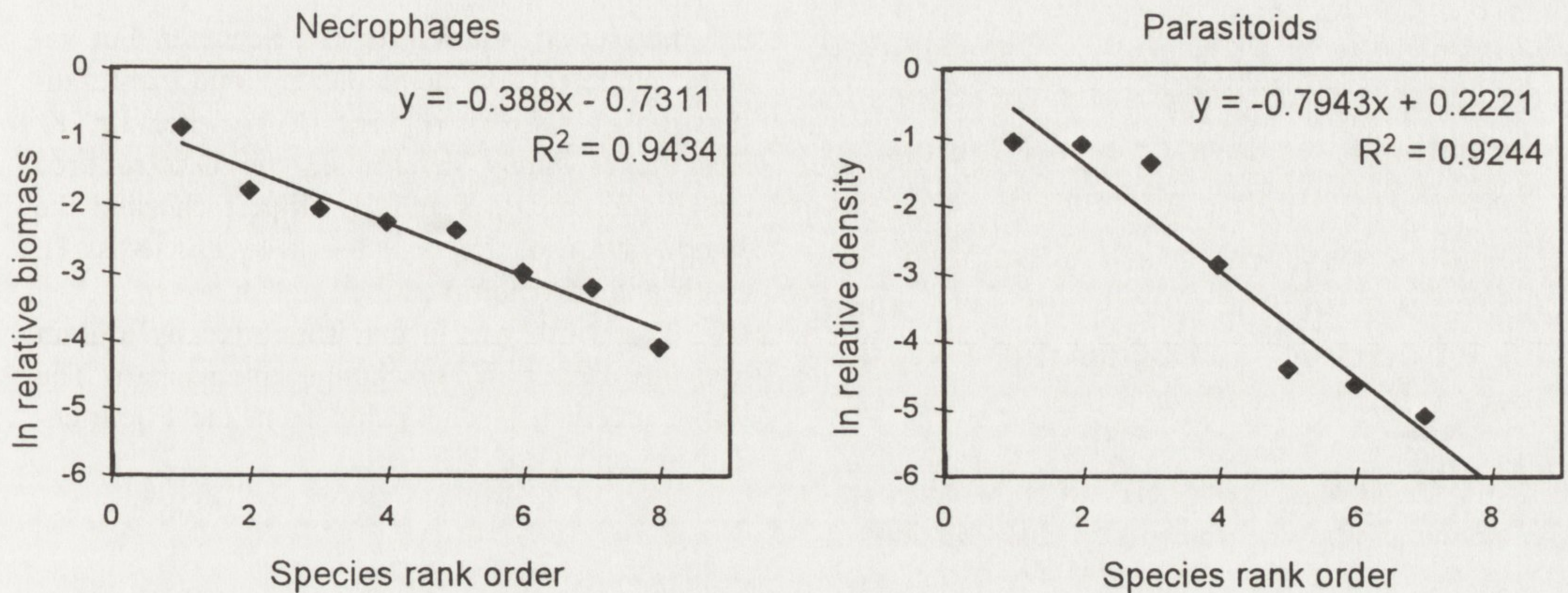
Fig. 10. Dominance rank order of necrophagous flies (judged by the biomass) and their parasitoids (abundance) which emerged out of dead *Arion ater*.

Table 9. Differences and similarities in the ecology of necrophagous Diptera and their parasitoids (Hymenoptera). Summary of the results of the breeding experiments with dead *Arion ater*.

Necrophagous Diptera	Parasitic Hymenoptera
Large number of species	Large number of species
Moderate species rank order	Pronounced species rank order
Higher diversity	Lower diversity
Colonization susceptible to desiccation of the carcass	Parasitism fairly independent of carcass desiccation
Densities of early colonizers do not depend on the weight of the carrion	Parasitism rates independent of the weight of the carrion
Densities of late colonizers correlate positively with the weight of the carrion	Parasitism in dominant species is not density dependent
–	Tendency of inversely density dependence in recedent species
Low interspecific competition	Pronounced interspecific competition only at high parasitism rates
High competition between the necrophagous flies and large predators and necrophages	–
High impact of large predators and necrophages on the mortality rates	Parasitism rates not influenced by the presence of larger competitors of the hosts
High degree of aggregation in the populations	High degree of aggregation in the populations
Negative correlation between abundance and degree of aggregation	No marked correlation between abundance and degree of aggregation
Aggregation of late colonizing species negatively correlated with the weight of the carrion	Aggregation independent of the number of hosts

competition is quite low. They showed only weak density dependent reactions to the amount of substrate or the number of hosts. The main differences are the greater susceptibility of the flies for drying-out of the substrates and their higher diversity and better niche separations.

5. SUMMARY

In a beech forest on limestone (FRG), the community of carrion (dead *Arion ater* slugs) exploiting Diptera and their parasitoids (Hymenoptera) was studied.

The carcass sustained a high number of species (Table 1; Figure 1, 2). 17 Diptera and 12 Hymenoptera were found. *Panorpa* sp. (Mecoptera), some Silphidae (especially *Necrophilus subterraneus*) and Carabidae (*Carabus coriaceus*) and *Arion ater* also fed on the dead slugs.

The degree of niche overlap of the fly and wasp species was large (Table 2, 3, 5; Figure 1). With the exception of *Kleidotoma psiloides* (Eucoilidae), all of the parasitoid species bred were polyphagous and attacked all of the fly species present (Table 5).

The populations of the fly and wasp species were highly aggregated (Figure 6). The degree of aggregation depended in an inversely manner on the density. High parasitism rates were correlated with lower degrees of clumping (Figure 9). The dispersion of the parasitoids was independent from the number of hosts. Diptera, which lay their eggs in a late stage of decay (Figure 3), showed a negative correlation between aggregation and the weight of the slugs (Figure 5).

There was no interspecific competition detectable between the fly species (Table 2, 3). The parasitoids did compete markedly only at high levels of parasitism (Table 7, 8). This resulted in a more pronounced species rank order of the parasitoids (Figure 10). For one parasitoid species, the degree of interspecific competition against other species was positively correlated with host density.

The parasitoids showed only a weak (negative) density dependent reaction to the number of hosts present (Table 6). The degree of density dependence was more pronounced in the more infrequent species. The total parasitoid numbers increased in a linear manner with increasing host densities, and therefore the overall parasitism rate was roughly constant for different host numbers (Figure 7, 8).

Large predators and necrophages (Silphidae, Carabidae, *Arion ater*) had a high impact on the mortality of the flies and wasps (Figure 4). In experimental boxes that allowed free access to these species, they totally prevented the development of phorid flies and their parasitoids.

The necrophagous flies were highly susceptible to drying out of the carcass, but the parasitism rates were not affected (Figure 3).

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