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Ecological Separation, Functional Relationships, and Limiting Resources in a Carrion Insect Community

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With 10 Figures

Abstract

1. The ecological separation of 19 carrion insect species (adults and some of their larvae) was investigated at rabbit carcasses in North Bavaria (FRG) referring to 4 niche dimensions. In the (1.) macrohabitats (forest — clearing) the distribution of saprophageous beetle larvae was mainly considered, for (2.) seasonality the differential abundance of blow flies (Colliphoridae). (3.) The stages of decay were correlated with the temperature dependent development of blow fly maggots affecting the abundance of competing saprophageous beetles and of carnivors preying upon maggots of different size classes. By using (4.) microhabitats (spatial subdivision of a carcass) as further niche dimension, the clustering of species using similar food resources was demonstrated in a niche overlap dendrogram.

2. The quantitative effect of predators on blow fly maggots was investigated both in field and laboratory experiments. Predation upon maggots reduces their scramble competition, resulting in a higher pupal weight. Thus, the reproductive success of the blow flies seems to be buffered by the developmental flexibility of the calliphorids. The numerical effect of predators and parasitoids on the blow fly *pupae* was also quantified.

3. In a case study on the staphylinid beetle, *Aleochara curtula*, we investigated the differential abundance of sexes. The ratio at which the males and females arrive at the carcass is balanced. Here the beetles feed and copulate. Females depart into the vicinity of the carrion much earlier than males, thus shifting the sex ratio to a male bias. In the surroundings the females deposit their eggs, and the parasitoid first instar larvae search for scattered blow fly pupae. The temporal and spatial distribution of both sexes of *A. curtula* is thus not only affected by the food allocation of the adults, but also by limiting resources of mating end egg laying sites as well as larval hosts.

1. Introduction

Carrion is commonly assumed to be a rare resource of patchy distribution, transient nature, and short supply. The process of decay is accompanied by a succession of insect communities with a great richness of species. Many efforts have been made to

find the relevant niche dimensions of ecological separation, for example, the various stages of decay, macrohabitats or season (FULLER 1934; CHAPMANN and SANKEY 1955; BORNEMISSZA 1957; WALKER 1957; REED 1958; PAYNE 1965; WASTI 1972; JOHNSON 1975, MCKINNERNEY 1978; TOPP et al. 1982). Similar approaches have been made in exemplarily studies on dung inhabiting beetles (HANSKI and KOSKELA 1977, 1979; KOSKELA 1972; KOSKELA and HANSKI 1977).

Surprisingly, a very important mechanism of ecological separation of carrion insects, the differentiated use of food resources, has been cited by only a few investigators (PAYNE and CROSSLEY 1966; SCHOENLY and REID 1983). This might be due to the lack of detailed knowledge on the life habits of the various species involved. We investigated, to which extent different spatial and temporal gradients correspond to the use of different food.

Ecological separation is a result of competition for a limiting resource. Carrion in our region is predominantly exploited by blow fly maggots. Their competitive interactions have been subject to numerous quantitative investigations (DENNO and COTHRAN 1975; HANSKI and KUUSELA 1977; HANSKI 1976; BEAVER 1977; KUUSELA 1983, 1984; KNEIDEL 1983, 1984; JOSWIG 1985). The concentrated occurrence of the saprophageous maggots was cited to attract a variety of predators (FULLER 1934; CHAPMAN and SANKEY 1955; REED 1958; PAYNE 1965; MCKINNERNEY 1978; PUTMAN 1978). Do these predators compete for maggots as a limited resource? The abundance of carnivors can not solely be used a measure for their influence on the population of prey species. Only a few investigations refer to the quantitative effect of predator-prey interactions in carrion insect communities (NUORTEVA 1970; LIPKOW 1982). We investigated the influence of carnivors on the maggot population by manipulating the access of predaceous insects in the field and by laboratory experiments under standardized conditions.

Is food the only limiting resource for adults of the different species? Carrion also provides (1.) places for mates to rendezvous, (2.) oviposition sites, and (3.) prey or hosts for larvae of different life habits. Therefore, the critical niche dimension is not identical for different developmental stages. It may also be different for both sexes, and change during the course of the succession or throughout the seasons, depending on reproductive cycles. In a detailed case-study of one species we investigate these factors, which affect the evaluation of abundances.

The insect of our choice is the staphylinid beetle, *Aleochara curtula* (GOEZE). The larvae are parasitoids of blow fly pupae (KEMNER 1926; PESCHKE and FULDNER 1977). In contrast to parasitic wasps, where females lay their eggs directly to the hosts, the beetles' first instar larva itself searches for a host puparium, gnaws an entrance hole into its wall, and lives inside as a solitary parasitoid. Orientation and competition of larvae, as well as mating behaviour of adults have been extensively investigated (FULDNER 1968; FULDNER and WOLF 1971; PESCHKE 1978a, b, 1979, 1983, 1985a, b). Essential behavioural aspects of this species, as foraging for food, mating, and egg laying may be affected by the special problems of carrion utilization. In a series of further investigations (PESCHKE et al. 1987a, b), we will report data on the autecology of *A. curtula* and the adaptations of imaginal and larval behaviour to the requirements of their parasitoid life cycle.

2. Materials and Methods

2.1. Study sites and carcasses

Field investigations were carried out from 1976 to 1983 at Erlach (near Würzburg, Northern Bavaria, FRG). For comparison of different macrohabitats, carcasses were exposed in shady deciduous forest on sandy soil and in sunny clearings with young pines (< 0.5 m height) and large open areas with scarce vegetation. A further site for experiments were grasy fields in the University's Botanical Garden, where the carcasses were exposed to direct sunlight; the underground (loamy soil) was free of vegetation. All rabbits (approx. 2,800 g), guinea pigs (500 g), rats (330 g) and mice (20 g) were obtained from laboratory strains, killed by CO_2 and stored frozen. Hoods of wire-netting ($80 \times 80 \times 65$ cm, 3 cm mesh) were fixed over the carrion by tent-pegs, in order to keep vertebrate scavengers away. The carcasses were deposited onto a wire netting (1 cm mesh), which was placed on a leveled and vegetation free area. Insects of all sizes had free access to the corpse. Temperature and relative humidity in the different habitats were continuously recorded by thermohygrographs.

2.2. Records of carrion insects

At least every two days the carcasses were examined to determine the actual stage of decay. All externally visible insects were recorded according to species and number of individuals. By lifting the wire-netting, all the insects, which were located on the soil and under the carcass were recorded. The carcass was shaken over a plastic box to lay hold of insects falling out of cavities within the carrion. The corpse was again deposited at the same site and all insects were put back, and most of them crawled back under the carrion or into its cavities. Only a few individuals were observed to escape after handling. We only took a very few specimen from the carcass in order to determine the species, because we wanted to observe live beetles in their microhabitat while feeding, without effecting the decaying process or the succession by manipulation. The larger species were well known from preliminary experiments at other carcasses, where all insects had been removed. Many small species, for example Aleocharinae, were neglected in quantitative analysis. Beetles were identified after FREUDE et al. (1964—1979) and flies after ZUMPT (1956). For some genera (e.g. *Hister*, *Philonthus*, *Necrophorus*, *Thanatophilus*) the species catalogued in Fig. 1, 2, 3, 5, and 6 as well as in Tab. 2 are the predominant members (> 90%). These species are referred to if only the genus name was used. Other congeneric species (see Tab. 1) are rare in our study area; their abundances were added to those of the dominant species.

For calculation of relative abundances in stages of decay the number of individuals of each species was summarized for each stage and related to 100% for the stage with maximal abundance. The relative abundance in different microhabitats was used for calculation of niche breadth ($NB = -\sum p_{ij} \ln p_{ij}$) and niche overlap ($NO = 1 - 0.5 \sum |p_{ij} - p_{hj}|$) according to COLWELL and FUTUYMA (1971). A niche overlap dendrogram was constructed by using an unweighted average-linkage clustering (PIELOU 1984). The relative abundance of carrion insects in forests or clearings was calculated by pooling data for all carcasses at all serial stages. For calculation of the seasonal occurrence we pooled the number (N) of insects per week at carcasses in both macrohabitats and plotted the abundance in a $\log(N + 1)$ scale. For further statistical analysis see SACHS (1984; χ^2-test, MANN-WHITNEY-U-test, confidence limits).

2.3. Marking experiments with *A. curtula*

In experiments investigating the transit of *A. curtula* individuals and the duration of their stay at the carcass, the beetles were recorded every 2 d, sexed in the field (PESCHKE 1978a), and marked by dots of enamel paint. The beetles were allowed to quiet down in a cooled container with moist filter paper before they were released at the same carcass again. Following this procedure, the insects were observed to hide immediately in cavities within the carcass; only very few beetles escaped. The loss of labels was determined by using marked beetles exposed to field conditions in screened plastic boxes filled with soil and provided with cut maggots (4×40 beetles; 87% loss of labels in 10 d). To determine the number of beetles, which roamed the vicinity of the carcass, 6 or 12 pitfall traps were installed at a distance of 60 cm from the carcass. The pitfall traps were made of plastic tubes (10 cm height, 5 cm diam., inlet funnel, bottom nylon grid). The live beetles were

recorded daily, sexed and released at the same distance from the carcass where they had been caught.
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2.4. Records of blow fly maggots and puparia

. After the emigration of maggots from the carcass small samples of soil from the carrion surroundings were checked for pupation of maggots. We then took adjacent soil samples of 20×20 cm and a depth of 7 cm in one or two straight lines from the carcass up to a distance of 3 m. The hand-collected puparia were checked for parasitation. Puparia were stored in sawdust to determine the number of hatching flies or parasites.

2.5. Laboratory experiments

Calliphora erythrocephala and *A. curtula* were reared by using standard laboratory techniques (PESCHKE et al. 1987a). Other carrion insects were freshly caught in the field and individually observed in plastic boxes (10×10×7 cm), the bottoms of which were covered with moist filter paper. Different diets (eggs, larvae and puparia of *C. erythrocephala*, beef liver) were offered together to individual beetles over a period of several days, during which we observed the feeding behaviour. The width of spread mandibles was determined from live beetles by using an ocular micrometer scale of a stereoscopic microscope.

3. Results

3.1. Ecological separation: temporal and spatial distribution of carrion insects

For a first evaluation of ecological separation among carrion insects we investigated their abundance and distribution along temporal and spatial niche gradients. First we considered coarse gradients of season and microhabitat, fine gradients like stages of decay or microhabitats were then investigated with special regard to the differential use of food resources. In 1976, we observed in our study area at Erlach 71 insect species at 10 rabbit carcasses (Tab. 1). For a quantitative analysis, we considered 19 of the most abundant species (8,210 individuals).

Habitat specialization, trophic levels, and developmental stages

Before we describe various resource gradients, some general ecological characterizations of the involved species are necessary. Most of these insects are carrion specialists, for example the calliphorids, *Dermestes*, or *Necrophorus*. On the other hand, some are not only restricted to carcasses. For example, *Geotrupes* and *Ontholestes* are regularly found in dung. Besides the problem of quantifying the degree of habitat specialization of the insects, the trophic level also can not be clearly defined for some of these insects. The classification in Fig. 1 (S: saprophageous, P: predaceous) gives only a rough estimation of the trophic level. Whereas blow fly maggots are definitely saprophageous insects as well as *Creophilus* is a predaceous beetle, other species like the adults of *Thanatophilus* and *Necrophorus* feed on maggots as well as on decaying meat. In addition, the feeding habits and distribution in time and space be different for adults and larvae. We therefore considered the larvae of some common species, for which quantitative records are easily possible, as distinct "ecospecies". Some of the species, which as adults feed on a variety of foods, have exclusively saprophageous larvae (*Thanatophilus, Oeceoptoma*).

Table 1. List of all insect species observed at rabbit carcasses in the experimental area of Erlach (near Würzburg, North Bavaria, FRG). Most abundant species of the genus marked by asterisks.

Coleoptera

Silphidae
  Silpha carinata HERBST
  Oeceoptoma thoracica L.
  Thanatophilus sinuatus FAB.
  Thanatophilus rugosus L.
  Necrophorus vespilloides HERBST
  Necrophorus vespillo L.
  Necrophorus investigator ZETTERSTEDT
  Necrophorus fossor ERICHSON
  Necrophorus humator OLIVIER
  Necrodes littoralis L.

Catopidae
  Catops tristis PANZ.
  Catops kirbyi SPENCE
  Catops neglectus KR.

Staphylinidae
  Staphylinus caesareus CED.
  Ontholestes murinus L.
  Ontholestes tesselatus GEOFFR. FOURCR.
  Creophilus maxillosus L.
  Philonthus politus L.
  Philonthus carbonarius GYLL.
  Philonthus chalceus STEPH.
  Philonthus addendus STEPH.
  Philonthus laminatus CREUTZ
  Philonthus coruscus GRAV.
  Philonthus varians PAYK.
  Philonthus sordidus GRAV.

  Aleochara curtula GOEZE
  Aleochara lata GRAV.
  Aleochara ripicola MULS. REY
  Aleochara brevipennis GRAV.
  Aleochara inconspicua AUBE
  Aleochara villosa MANNERH.
  Aleochara bipustulata L.

  Nehemitropia sordida MANNERH.
  Proteinus spec.
  Phyllodrepa translucida KR.
  Oxytelus sculpturatus GRAV.
  Oxytelus rugosus GRAV.
  Xantholinus spec.
  Tachinus spec.

Histeridae
  Hister cadaverinus HOFFM.
  Hister unicolor L.
  Hister striola SAHLB.
  Saprinus semistriatus SCRIBA

  Paralister carbonarius HOFFM.
  Paralister purpurascens HBST.

Scarabaeidae
  Geotrupes stercorarius L.
  Trox sabulosus L.
  Trox scaber L.
  Onthophagus ovatus L.
  Onthophagus coenobita HERBST

Dermestidae
  Dermestes murinus L.
  Dermestes lardarius L.
  Dermestes undulatus BRAHM.
  Dermestes frischi KUGEL.

Cleridae
  Necrobia violacea L.

Nitidulidae
  Omosita discoidea FABR.
  Omosita depressa L.
  Nitidula carnaria SCHALLER
  Glischrochilus quadripunctatus L.

Tenebrionidae
  Stenomax aeneus SCOP.

Hymenoptera

Ichneumonidae

Braconidae
  Alysia manducator PANZ.

Eucoilidae

Chalcididae

Formicidae
  Lasius niger L.

Vespidae
  Paravespula vulgaris L.

Sphecidae
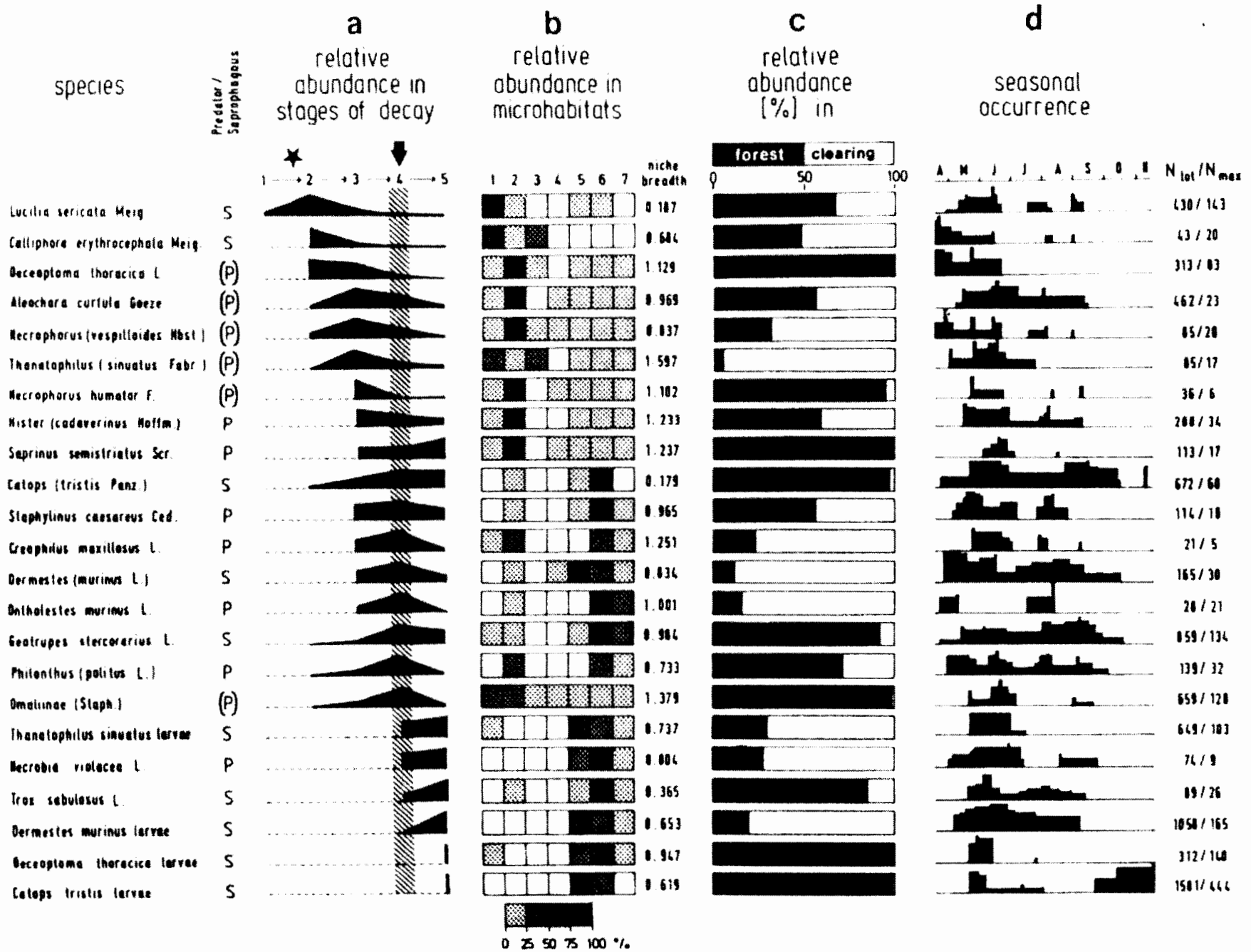 *Mellinus arvensis* L.

Diptera

Muscidae
  Ophyra leucostoma WIEDEMANN
  Fannia canicularis L.

Calliphoridae
  Calliphora erythrocephala MEIG.
  Lucilia sericata MEIG.
  Cynomyia mortuorum L.

Sarcophagidae
  Parasarcophaga scoparia PAND.

	Predator / Saprophagus	**a** relative abundance in stages of decay	**b** relative abundance in microhabitats	niche breadth	**c** relative abundance [%] in	**d** seasonal occurrence	N_{tot}/N_{max}

species

a — relative abundance in stages of decay (1 → 2 → 3 → 4 → 5)

b — relative abundance in microhabitats (1 2 3 4 5 6 7) niche breadth

c — relative abundance [%] in forest / clearing (0 50 100)

d — seasonal occurrence (A M J J A S O N)

species	P/S	niche breadth	N_{tot}/N_{max}
Lucilia sericata Meig.	S	0.187	430 / 143
Calliphora erythrocephala Meig.	S	0.646	43 / 20
Oeceoptoma thoracica L.	(P)	1.129	313 / 83
Aleochara curtula Goeze	(P)	0.969	462 / 23
Necrophorus (vespilloides Hbst.)	(P)	0.837	85 / 28
Thanatophilus (sinuatus Fabr.)	(P)	1.597	85 / 17
Necrophorus humator F.	(P)	1.102	36 / 6
Hister (cadaverinus Hoffm.)	P	1.233	208 / 34
Saprinus semistriatus Scr.	P	1.237	113 / 17
Catops (tristis Panz.)	S	0.179	672 / 68
Staphylinus caesareus Ced.	P	0.965	114 / 18
Creophilus maxillosus L.	P	1.251	21 / 5
Dermestes (murinus L.)	S	0.834	165 / 30
Ontholestes murinus L.	P	1.001	28 / 21
Geotrupes stercorarius L.	S	0.984	859 / 134
Philonthus (politus L.)	P	0.733	139 / 32
Omaliinae (Staph.)	(P)	1.379	659 / 120
Thanatophilus sinuatus larvae	S	0.737	649 / 103
Necrobia violacea L.	P	0.804	74 / 9
Trox sabulosus L.	S	0.365	89 / 26
Dermestes murinus larvae	S	0.653	1050 / 165
Oeceoptoma thoracica larvae	S	0.947	312 / 148
Catops tristis larvae	S	0.619	1501 / 444

forest | clearing

0 25 50 75 100 %

The functional role of vertebrate scavengers was not taken into account in the present study, because the carcasses had been protected by hoods of wire-netting. From a series of 86 rats, which were *not* protected, we lost 70 by larger vertebrate scavengers (probably foxes, rats, jackdaws or jays); 14 were burried by *Necrophorus*. At only two unprotected carcasses maggots could develop until pupation. In contrast, in all 11 rat carcasses covered by wirenettings we observed complete blow fly development.

Macrohabitats

We deposited rabbit carcasses in forests or clearings and calculated the relative abundance of insects found in both macrohabitats (Fig. 1c). In 21 out of 23 species (adults and larvae), we found a significant preference for one of the macrohabitats. Thirteen of them were more abundant in forests. Some silphid beetles are restricted to forests *(Oeceoptoma)* or clearings *(Thanatophilus)*. As a striking example, the larvae of saprophageous beetles show a very different distribution in both sites (Fig. 2). Among the predators, macrohabitat preferences are less conspicuous: *A. curtula*, *Hister*, and *Staphylinus*, for instance, are more or less evenly distributed in both sites.

Season

A further mechanism for ecological separation of carrion insect is seasonality (Fig. 1d). Some species were found throughout the year (e.g. *Geotrupes* and *Catops* adults), whereas others mainly occur in spring (e.g. *Oeceoptoma*) or autumn (e.g. larvae of *Catops*) or have clearly separated peaks of abundance in spring and summer (e.g. *Ontholestes*).

Among the blow flies, *Calliphora* was a spring species, whereas *Lucilia* was more abundant during summer. The seasonal change of dominant blow fly species was also clearly visible in the relative abundance of puparia, which were collected from soil samples from under the carcass and up to a distance of 3 m (Fig. 3).

Stages of decay

Species, which occur at carcasses in the same macrohabitat and season may be separated by their different time of occurrence during the short period the carrion is available. In order to describe the variable conditions at a carcass in the progress of decay, distinct stages have been defined by many authors using physical and chemical criteria. We follow the classification of REED (1958) and PAYNE (1965):

Fig. 1a—d. Occurrence of predaceous (P) and saprophageous (S) insects at exposed rabbit carcasses relative to various niche dimensions: *(a)* Stages of decay: (1) fresh, (2) bloated, (3) active decay, (4) advanced decay, (5) dry; graphs were related to the stage with the maximal abundance; asterisk indicates egg deposition of calliphorid flies; arrow (along with shaded area) the period of migration of postfeeding maggots. *(b)* Microhabitats at the carcass: spatial distribution in resource classes 1—7 (see text) and niche breadth. *(c)* Macrohabitats: relative abundance at carrion exposed in forest or clearing. *(d)* Season: log $(N + 1)$ individuals observed per sample. N_{tot}: total number of observed individuals; N_{max}: maximal number of individuals ever observed in one sample. Species names in brackets represent the most abundant species of the genus (see text and Tab. 1).
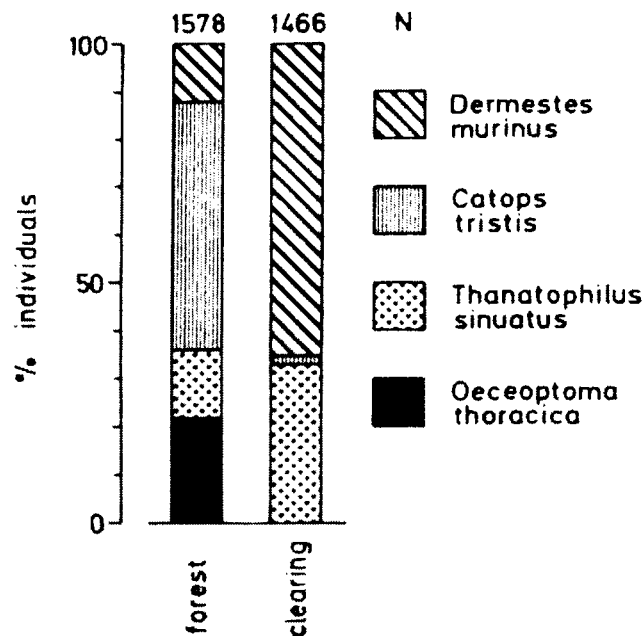
Fig. 2. Relative abundance of saprophageous beetle larvae at rabbit carcasses exposed in forest (N = 5) and clearing (N = 5).
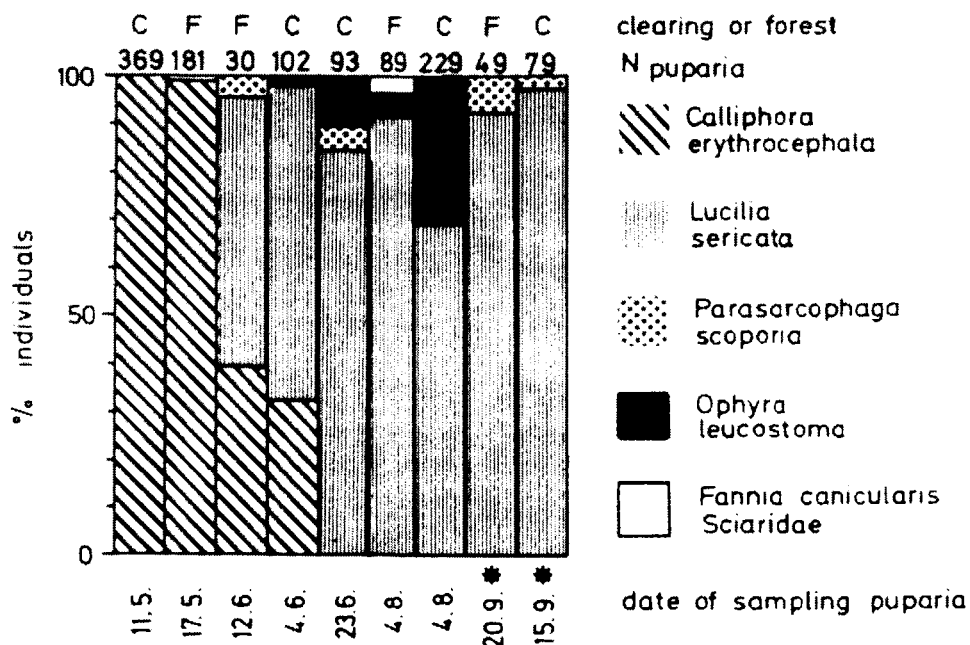

Fig. 3. Relative abundance of fly pupae collected at subsequently exposed rabbit carcasses in soil samples from beneath the carcass and up to a distance of 3 m. Asterisks indicate samples, where *Lucilia sericata* was found to hibernate as a prepupa.

(1) *Fresh stage*. Body specific odour of the freshly exposed carcass:

(2) *Bloated stage:* The body is bloated by fermentation, liquids leak from mouth, nose and anus; a sweetish odour changes to the typical odor of decay:

(3) *Stage of active decay:* Muscles lay open: the fur falls out in tufts: ammoniac stench of decaying meat reaches its maximum:

(4) *Stage of advanced decay:* Muscular tissue is almost consumed; only greasy remnants from viscera: shape of the carcass totally disintegrated; fur mixed up with grubbed soil: smell of ammoniac:

(5) *Dry stage:* The remnants (fur, skin, bones and tendons) dry out and mummify or — under humid conditions — keep moist for a long period and emit a moldy odour.

The sequence of stages of decay is accompanied by a succession within the carrion insect community. In Fig. 1a the species are arranged according to their maximal abundance during the progress of decay.

Among the saprophageous insects, blow fly maggots apparently play an essential role in carrion decomposition in our region. Their development marks significant incisions in the course of the succession. (1) The eggs of the dominant species *L. sericata* and *C. erythrocephala* are layed in the first and second stage of decay; (2) the fully grown maggots disintegrate the carcass in the third stage of succession. After feeding they gather to form a whirling mass under the carcass and empty their guts. (3) Most of the maggots ($> 90\%$) leave the carrion within a short period of several hours and pupate in the surroundings. A few remaining maggots represent late-comers, individuals parasitized by Hymenoptera, and those of other fly species (*Fannia, Ophyra,* Fig. 3).

The duration of the decaying process depends on climatic conditions. For the first stage minimal and maximal durations were 0.5—4 d; for stage 2: 0.5—9 d; stage 3: 3—16 d; stage 4: 2—15 d. It was not possible in our investigations to define the end of the 5th stage or a transition to the 6th stage proposed by PAYNE (1965). The time from the exposure of the carrion to the end of stage 4 is fourfold shorter if the average temperature during the succession is increased from 10 to 22 °C (Fig. 4a). In the same way the speed of maggot development is increased, as measured by the time from exposure of the carrion to emigration of postfeeding maggots (Fig. 4b) or the time from migration to pupation (Fig. 4c).

During the feeding period of calliphorid larvae, only a few other saprophageous insects are present *(Geotrupes, Dermestes, Catops).* After emigration of maggots, however, saprophageous beetles and especially their larvae become very abundant (Fig. 1a).

The occurrence of carnivorous beetles is correlated with the abundance of their prey. Because blow fly maggots as the predominant prey grow very quickly and synchronously, a temporal succession of predators of various size could be expected. We observed the feeding behaviour of some dominant predators in the field as well as in laboratory cultures by offering various foods (Tab. 2). The species in the table were arranged according to their width of mandibles, which was expected to be closely related to their food preference. The smallest predators were Omaliinae, feeding on fly eggs and newly hatched maggots. Medium sized beetles prey upon medium sized maggots and avoid entering the concentrated bulk of feeding blow fly larvae. They mainly stay under the carcass. Fully grown maggots could only be overwhelmed by rove and hister beetles. They picked up postfeeding maggots prior to migration from the periphery of the carcass or attacked migrating individuals. Only *Creophilus* was able to break open puparia of blow flies.

However, there is not always a correlation between the occurrence in a certain stage of decay and the width of spread mandibles. This might be due to the fact that some predators have an additional food supply. Silphidae and some small and medium sized rove beetles also feed on decaying meat. Some large rove beetles preyed upon larvae of saprophageous beetles. *Staphylinus* even refused maggots in the laboratory.
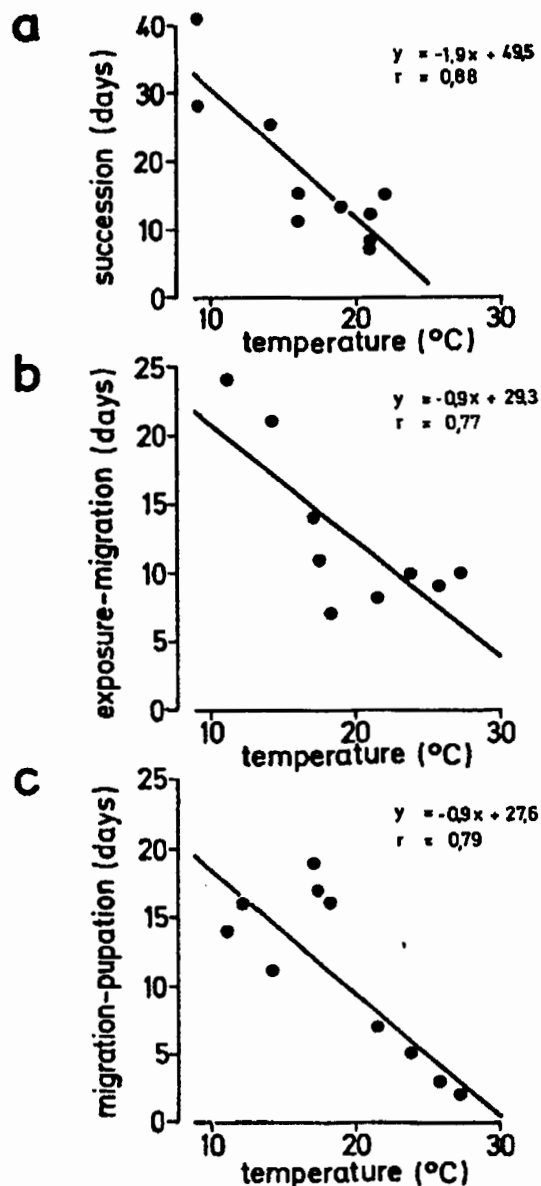
Fig. 4a—c. Duration of decay and development of blow flies at 10 rabbit carcasses depending on the mean temperature. *(a)* Period from carrion exposure to end of stage 4 (advanced decay). *(b)* Period from carrion exposure to migration of postfeeding maggots. *(c)* Period from migration of maggots to pupation. Linear regression analysis.

We therefore assume a prey specialization in this beetle, which was observed to feed on larvae of *Dermestes* and *Thanatophilus* in the field.

Microhabitats

Some species occurred throughout consecutive stages of decay, but were restricted to certain sites at the carcass. For example, *Dermestes*, a beetle typical for advanced stages of decay, has been observed on the dry skin of legs and ears of rabbits, while the moist core of the same carcass was filled with medium sized maggots and the carrion as a whole had to be classified as belonging to an early serial stage. The stages of decay represent means of different qualities, observed at a certain time. We additionally investigated the spatial distribution of these defined qualities independent from time.

Table 2. Preferred food of carrion inhabiting beetles (imagines) after field observations and laboratory feeding experiments. —: no evidence; +: occasional observation; **+**: preferred food, with particular support from field observations

Predator	Width of mandibles x ± SD	eggs	small	medium	large	puparia	larvae of saprophageous beetles	decaying meat
Omaliinae	0.7 ± 0.3	**+**	+	—	—	—	—	**+**
Aleochara curtula	1.3 ± 0.1	+	+	**+**	+	—	—	**+**
Hister cadaverinus	1.4 ± 0.2	+	+	+	**+**	—	—	+
Thanatophilus sinuatus	2.3 ± 0.1	—	+	**+**	—	—	—	**+**
Oeceoptoma thoracica	2.5 ± 0.1	+	+	**+**	—	—	—	**+**
Philonthus politus	3,3 ± 0.5	+	+	**+**	+	—	—	+
Necrophorus vespilloides	3.6 ± 0.3	—	—	+	**+**	—	—	**+**
Staphylinus caesareus	3.8 ± 0.9	—	—	+	+	—	**+**	—
Ontholestes murinus	4.4 ± 0.6	—	—	+	**+**	—	**+**	—
Creophilus maxillosus	7.5 ± 0.9	—	—	—	**+**	+	—	—

We therefore described 7 microhabitats at different regions of the corpse and its close surroundings. They provide a variety of microclimatic conditions and food qualities, which are arranged along an axis from the centre to the surroundings of the carcass, independent from the successional stages.

Definition of microhabitats:

(1) fresh meat, visible on the upper surface;
(2) decaying meat; under the carcass and in the soil beneath;
(3) at or in natural orifices;
(4) disintegrated viscera;
(5) moist fur and skin with remains of meat;
(6) dry skin, fur, bones, tendons;
(7) on the surface of the soil in the vicinity of the carcass.

The relative abundance of carrion insects in these microhabitats was determined (Fig. 1b). As extreme examples, adults of *Catops* and *Trox* with niche breadths of 0.170 and 0.365 were mainly found in microhabitat 6; on the other hand, Omaliinae were found distributed all over the microhabitats (niche breadth 1.379). In a niche overlap dendrogram (Fig. 5) all species were included irrespective of their trophic level. Species were clustered in 3 predominant groups. The species of group (A) were observed at drier parts of the carcasses and mainly represent saprophageous beetles and their larvae (except *Necrobia*, a predator on *Dermestes* larvae). In group (B) large carnivorous Staphylinidae and Histeridae were bunched together (except *Geotrupes*), whereas in group (C) those predaceous species were clustered which prefer moister parts of the carrion and feed on maggots as well as on decaying meat. Thus, the correlation
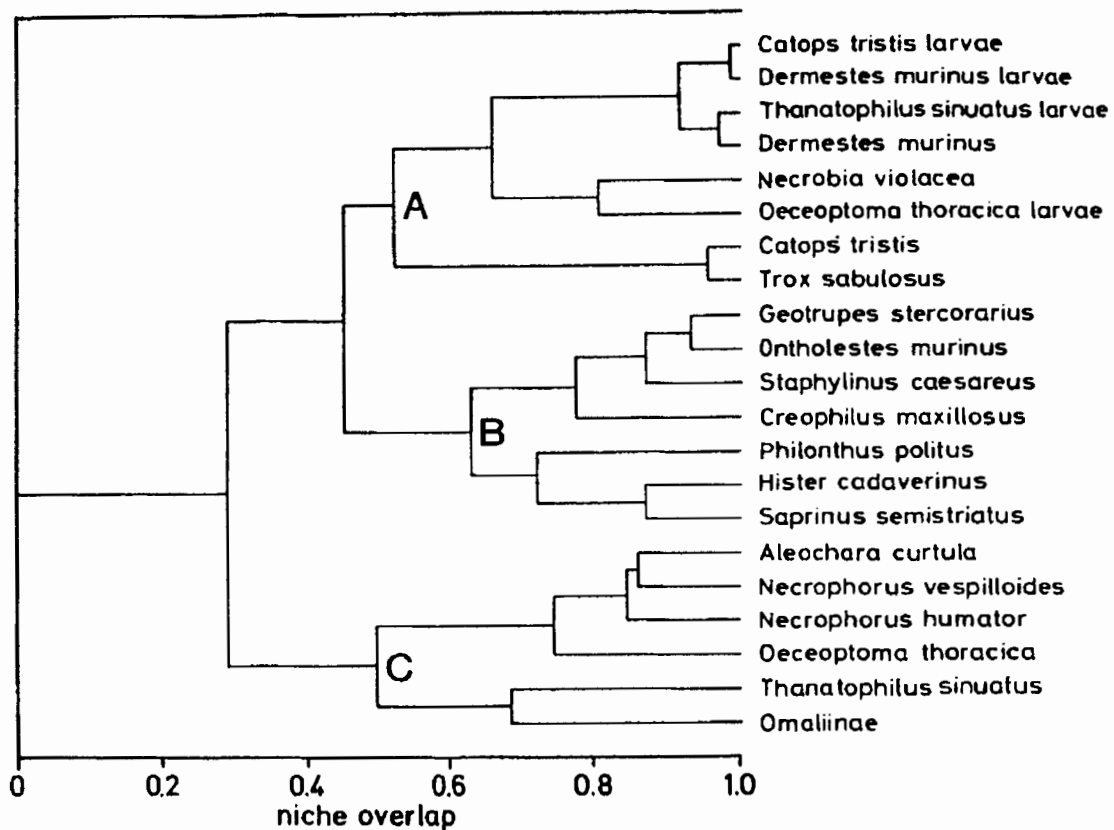
Fig. 5. Niche overlap dendrogram of carrion inhabiting beetles relative to their abundance in different microhabitats at the carcass.

between microhabitat and trophic level gives a solid base for the description of carrion insect communities.

3.2. Functional relationships of blow flies, predators and parasitoids

Since blow flies are the predominant saprophageous insects at a carrion, attracting many specialized carnivors preying upon them, we investigated the numerical effect of predators and the developmental responses of the maggots.

Nine rat carcasses were exposed at the same day at a distance of about 50 m from one another (June 1982). Three days after exposure, the blow flies *(Lucila sericata)* had laid most of their eggs. Then we brought 6 carcasses back to the laboratory, where all insects except maggots were removed by hand collection. The carcasses were kept in plastic containers (14×14×34 cm) on sandy soil. Three of them were not further treated; and to three other carcasses we added liver ad libitum (1,000—2,700 g) as an additional food supply for the maggots. Another set of three rats was exposed in the field for a longer period (8 days), and was then brought back to the laboratory just prior to maggot migration. After removing all other insects, the carrion together with maggots was incubated in the laboratory as described above but without adding any food. Four days after the larvae had left the carrion, the soil was sieved for maggots and puparia. Since pupariation did not take place in all individuals due to the artificially increased densities of *Lucilia* larvae, the number and total biomass was determined for both maggots and puparia (Tab. 3).

Table 3. Influence of predation and competition on abundance, total biomass, and average weight of emigrated maggots and puparia of *Lucilia sericata* developing at rat carcasses. The period of exposure to predation in the field was varied and competition for food was manipulated by additional supply of liver in the laboratory (for details see text).

Conditions	Carcass no.	Days exposed in the field	$N_{predators}$	Additional food for maggots	$N_{maggots}$ + puparia	Biomass (g) maggots + puparia	Average weight (mg) of maggots or puparia
Predation Competition	1	8	30	—	239	9	41.4
	2	8	135	—	980	26	27.0
	3	8	46	—	1,207	28	23.4
	mean				809	21	26.7
Reduced predation Competition	4	3	0	—	3,175	54	17.2
	5	3	1	—	6,078	56	9.2
	6	3	0	—	9,970	94	9.4
	mean				6,408	68	10.7
Reduced predation Reduced competition	7	3	5	+	8,375	165	19.8
	8	3	0	+	13,145	307	23.4
	9	3	2	+	16,617	314	19.0
	mean				12,712	263	20.8

When the carcasses were exposed for a long period (8 d), the fly population was reduced to an eighth part respective to number, or to a third part respective to biomass in comparison to carcasses exposed only a short period of time (3 d) without additional food (P = 0.05, MANN-WHITNEY-U-test). Predation seems to be the most important factor. We have no indication for other causes of mortality (e.g. bacterial deseases, desiccation of carrion). If predators had access, only 7% of the initial fresh weight of the rat carcass was found to be incorporated by maggots, whereas after removal of predators the production efficiency of blow fly larvae was increased to 21%.

When the competition among maggots for food is reduced by an additional food supply, the number of resulting maggots and puparia is nearly doubled, and the biomass is four times as high as in experiments without additional food, but where exposure to predators was very short (P = 0.05). In the carcass, where effects of both predation and competition were reduced, the number and biomass of the resulting maggots and puparia were ten times as high as in experiments where both factors were acting (long exposure, no additional food, P = 0.05).

Besides these striking tendencies, which were obvious comparing different sets of experiments, we observed an enormous variation in the number of blow flies developing at individual carcasses (Tab. 3). In other experiments, approximately 260, 700, 980,
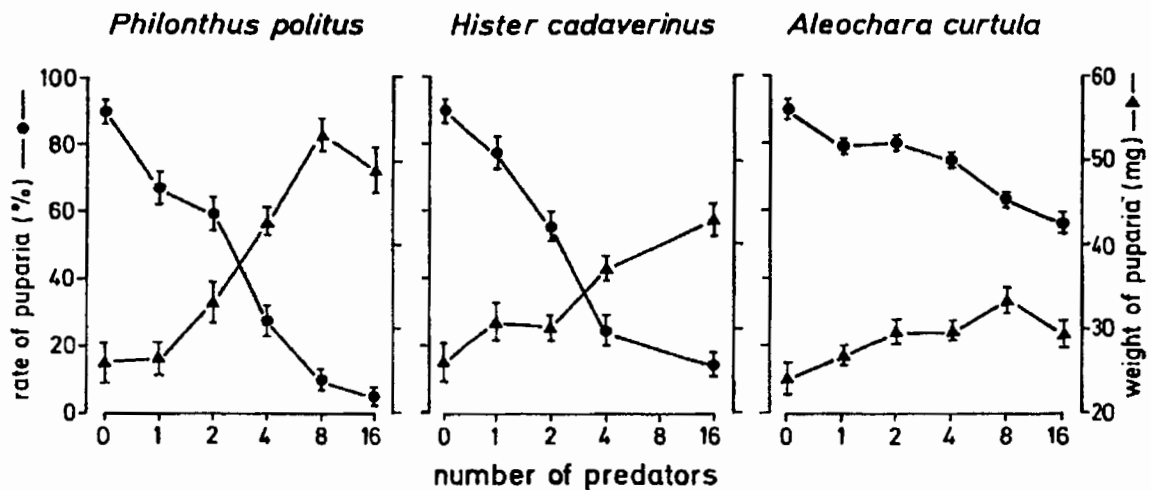
Fig. 6. Effect of increasing numbers of predator individuals *(Philonthus politus, Hister cadaverinus, Aleochara curtula)* on the rate of pupariation and mean weight of puparia (N = 30), resulting from 400 freshly hatched maggots of *Calliphora* added to an artificial carrion (20 g beef liver). Vertical bars: 95% confidence limits.

or 1,200 fly pupae were estimated to develop at 4 equal-sized rat carcasses from puparia collected in soil samples. We calculated about 15,350, 5,900, and 4,240 blow flies, respectively, to complete their development in the vicinity of three rabbit carcasses. This variation may not only be due to the number of blow fly eggs, but also to a variable number of predators (Tab. 3). In another experiment with 5 rat carcasses simultaneously exposed in the forest habitat at apparently similar sites (June 1980), we recorded maximal numbers of 20, 30, 44, 96, and 98 *A. curtula* individuals, respectively. Since the influence of predators in the field could not be exactly controlled by only manipulating their period of access, we also conducted laboratory experiments.

We collected the most abundant predators, *Aleochara*, *Philonthus*, and *Hister*, in the field and transferred them in increasing densities (1, 2, 4, 8 or 16) to carrion in the laboratory (20 g beef liver), and added 400 freshly hatched maggots of *Calliphora* to each set. These carcasses were stored at 22 °C in 1 l-jars half filled with sawdust. Ten days later the resulting puparia were counted; 30 of them were randomly withdrawn and weighed individually.

In control experiments without beetles, 90% of the introduced maggots developed to pupae, but due to intraspecific competition the puparia were very small (Fig. 6, control = 0 predator).

A group of 16 *Philonthus* and *Hister*, respectively, diminished the population of blow fly maggots nearly to zero (Fig. 6). However, the weight of resulting puparia was increased with the reduction of the number of individuals. A group of 16 *Aleochara* individuals reduced the number of puparia to only 56%. Here, the increase of the mean weight of the puparia was significantly lower than in experiments with the other predators.

Some mortality factors, for example the parasitation by Hymenoptera, only become evident in the field after the emigration of maggots and pupation. The effect of parasitoids and predators on these developmental stages of blow flies was calculated from puparia collected in soil samples taken in the vicinity of ten carcasses (Tab. 4). They

Table 4. Predation (Histeridae) and parasitation (Hymenoptera and *Aleochara*-species) on puparia of *Lucilia sericata*, collected from soil samples at 10 rabbit carcasses exposed from May to August in two experimental regions

Date of sampling	Erlach 1976							Botanical Garden 1978		
	May 17	May 24	June 21	July 28	July 30	Aug. 30	Sept. 3	June 18	July 21	Aug. 2
% normal development	92	82	99	96	77	39	33	35	77	92
% attack by										
Histeridae (larvae)	*	0	*	*	*	0	0	19	0	0
Hymenoptera**	2	18	0	2	21	61	67	19	18	3
A. curtula	6	0	1	2	2	0	0	16	3	2
A. bipustulata	0	0	0	0	0	0	0	11	2	3
$N_{puparia}$	67	17	79	82	160	74	48	220	611	963

* Attack on puparia not observed, but *Hister*-larvae collected in soil samples.

** 68% *Alysia manducator* (Braconidae), 21% Eucoilidae, 9% other Ichneumonidea, 2% Chalcididae.

developed to flies in 33 to 99%. The activity of hister beetle larvae, which destroyed up to 19% of the fly pupae, was determined by typical cracks in the puparium wall (LINDNER 1967). Parasitoid Hymenoptera from various taxa attacked blow fly puparia at rates up to 67%. In average, about 2% of the puparia were attacked by *A. curtula* larvae (max. 16%; entrance holes, FULDNER 1968). For three rabbit carcasses the total number of *A. curtula* individuals developing on fly pupae in the entire carrions' surroundings was estimated to be 100, 140 and 180, respectively. *A. curtula* larvae were found to attack pupae of *Lucilia*, whereas those of *Calliphora* (spring species) and *Parasarcophaga* (pupae directly at the carcass) were only attacked under laboratory conditions. Puparia of the secondary fly, *Ophyra* (late pupation), were found to be attacked by *A. curtula* larvae in the field, which, however, were not able to complete their development on this host. At some carcasses which were exposed in the botanical garden, we also found *Lucilia* puparia to be parasitized by *A. bipustulata* (up to 11%).

3.3. A case study: Differential abundance of sexes of *A. curtula*

It is commonly suggested that food is the critical resource for a majority of species. In addition, a habitat like carrion may also provide the place of rendezvous, the site for egg-laying, and food or hosts for larval stages. Thus, the abundance of a species may also be affected by differential requirements of sexes and reproductive cycles. We will demonstrate these complications for one intensely investigated carrion insect, the staphylinid beetle, *Aleochara curtula*.

A. curtula is a common species of rove beetles found in the palaearctic region and North America. Carcasses are the essential habitat of this species, and only occasional reports are made that the beetles use dung or decaying plants as alternative habitats
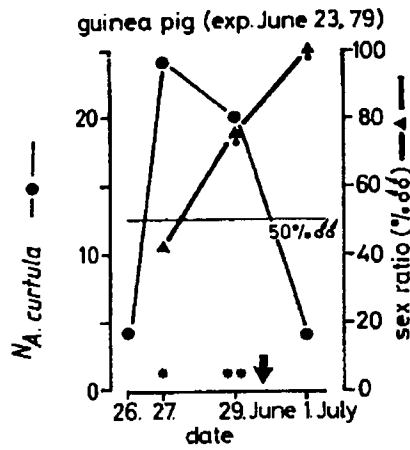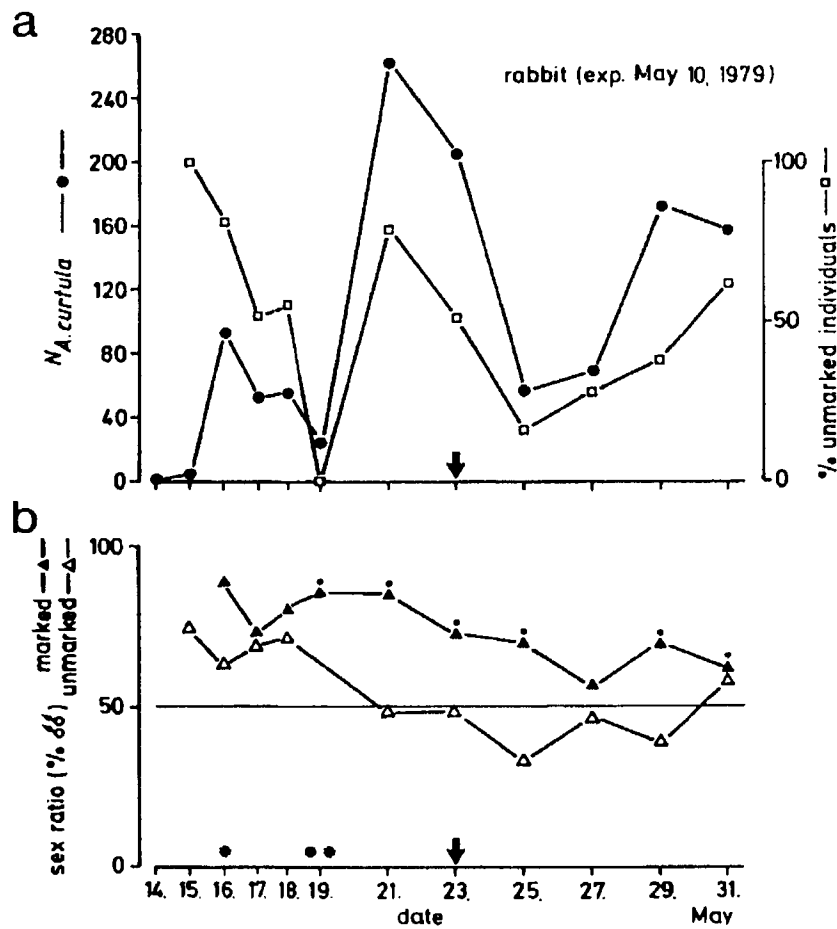
Fig. 7. Abundance and sex ratio of *Aleochara curtula* adults during the succession at an exemplary carcass exposed in summer. Dots at symbols indicate a significant difference to the 50 : 50 sex ratio (P < 0.05; χ^2-test). One asterisk: newly hatched maggots; two asterisks: fully grown maggots; arrow: emigration of maggots.

Figs. 8a, b. Abundance, sex ratio, and immigration of *Aleochara curtula* adults during the succession at an exemplary carcass exposed in spring with all freshly immigrated individuals marked. *(a)* Abundance of *A. curtula* and percentage of newly immigrated beetles; *(b)* sex ratio of marked and unmarked individuals. Explanation of symbols see Fig. 7.

(BERNHAUER and SCHEERPELTZ 1926; HORION 1967; KLIMASZEWSKI 1984). We found *A. curtula* at carcasses of various invertebrates and vertebrates ranging in size from snail to deer, and no preferences was found for a certain kind. However, the larger the carcasses of a series of different mammals were, the more beetles were attracted (8 rabbits: 49—262 *A. curtula* individuals; 8 rats: 3—98; 5 mice: 0—1). The adults feed on medium size maggots as well as on decaying meat. Reports on the widespread and common occurrence of *A. curtula* in different macrohabitats were given in the faunistic literature (HORION 1967). In our experimental area we could not find a striking preference for either forests or clearings (Fig. 1c).

The abundance of *A. curtula* during the succession varies extremely between individual carcasses ($N = 10$), not allowing the pooling of data or calculating means. We therefore illustrate the situation with two examples (Figs. 7 and 8). However, the tendencies observed here were valied for all carcasses. During constant summer conditions (Fig. 7), the peak abundance was observed to occur prior to the migration of maggots, when small and medium sized blow fly larvae were present. On the other hand, cool weather periods in spring slowed down the progress of decay, and the abundance of *A. curtula* did not show such a clear correlation to maggot development (Fig. 8a).

At one rabbit carcass (Fig. 8a) all *A. curtula* individuals were marked, each control with a color code specific for day and sex, and were released at the same carrion. The high rate of unmarked individuals in recaptures demonstrated the passing through of a large number of beetles during the succession. Even late after the migration of maggots, unmarked *A. curtula* individuals occurred. In this exemplary rabbit carcass 668 individuals passed through. The long lived beetles (up to 8 months in the laboratory) moved between successively exposed carcasses ($N = 11$), which were scattered at random at distances of 200—1,000 m from each other. Marked males ($N = 55$) were recaptured up to 41 d after labelling and up to a distance of 1,000 m (females $N = 22$; max. 37 d; 700 m). One individual marked in July, 1979 was found 10 months later after hibernation in May, 1980.

For experiments on the duration of stay of *A. curtula* individuals at the carcass, we sexed and marked laboratory bred beetles immediately after hatching. Males and females were separated and fed on maggots for a period of three weeks. Carcasses of guinea pigs had been pre-exposed to natural oviposition by blow flies and were then — after removal of all insects except of maggots — transported to the experimental area at Erlach (July 1979). Thirty *A. curtula* males and females, respectively, were released each group at another carcass. During the following days, we recaptured only a few females at the carcass at which they had been released (Fig. 9). Males, however, populated the carrion strikingly longer than females; 40% were recaptured even 10 d after their release.

During the early stages of the succession, the sex ratio at carcasses exposed in summer is balanced; however, just prior and after emigration of maggots, we predominantly captured males at the carrion (Fig. 7). In spring, the sex ratio is significantly skew throughout the whole succession (62% males, $N = 1,183$). If we differentiate between unmarked and marked individuals (Fig. 8b), no significant bias was observed in newly arrived beetles (in total: 56% males, $N = 668$), whereas the sex ratio of recaptured
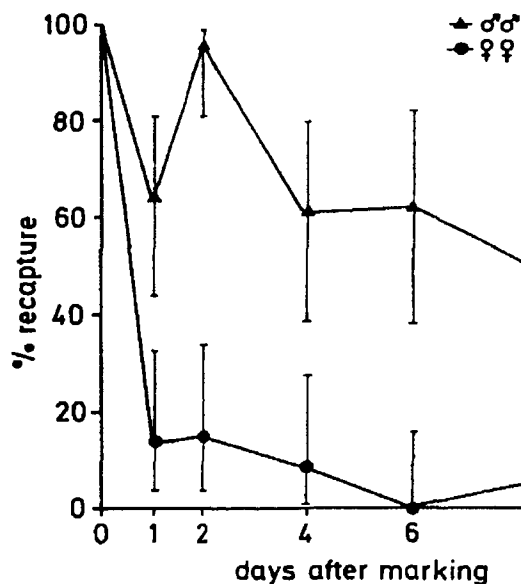
Fig. 9. Recapture of laboratory reared and marked males (N = 30) and females (N = 30) of *A. curtula* at the same carcass, where they had been separately released. Vertical bars: 95% confidence limits.
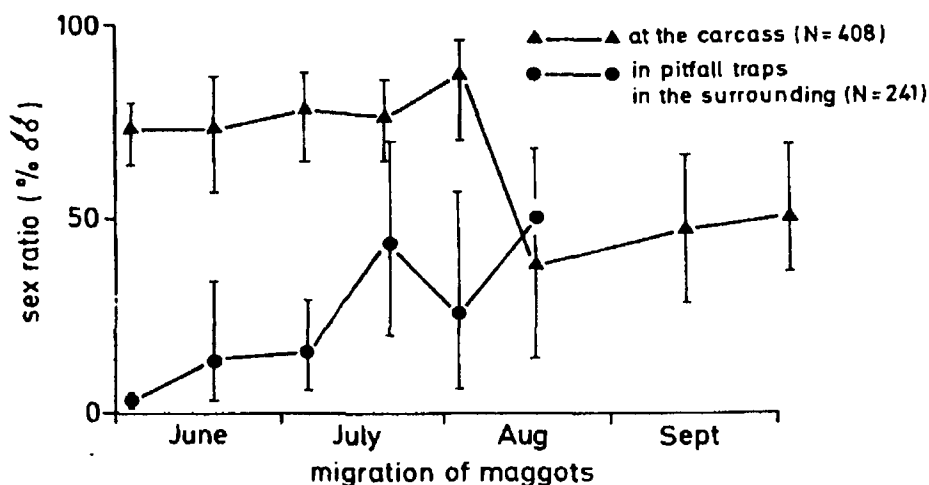

Fig. 10. Sex ratio of *A. curtula* directly at the carcass and in pitfall traps at a distance of 60 cm from the carrion relative to their occurrence at 8 subsequently exposed rabbit carcasses during maggot migration. Vertical bars: 95% confidence limits.

individuals was 71% males (N = 429). In laboratory cultures, the sex ratio of emerging beetles was balanced (52% males, N = 3,429).

A. curtula was mainly found under the carcass on decaying meat (microhabitat 2; 71%), but also in the surroundings of the carcass (microhabitat 7; 12%; Fig. 1b). In order to investigate possible differences in the abundance of both sexes in the microhabitats, we collected beetles during May and June directly at carcasses and in pitfall traps which were buried 0.6 m from the carcass. During the total succession fifty samples (N = 3,320) from 10 carcasses were taken and pooled. 63% of the *A. curtula* individuals found at the carrion were males, whereas 80% of the beetles found in the surroundings were females. The number of *A. curtula* caught in pitfall traps in the surroundings declined in late summer. Simultaneously, the sex ratio of beetles in the

traps as well as at the carrion was shifted to 50:50 (Fig. 10). In this period, the reproductive activity terminates: Copulations were only seen from May to July, and first instar larvae or parasitized blow fly puparia were found from June until the midth of August. On the other hand, A. curtula adults were baited for a much longer period (April through October).

4. Discussion

4.1. Ecological separation

Carrion is a habitat characterized in particular by its temporal limitation and the fast alterations of the availability of various resources. Temperature affects desiccation, chemical reactions, microbial activity as well as the metabolism of saprophageous insects. Thus, the duration of microserial stages clearly depends on varying climatic conditions during the course of the seasons and on sudden weather changes. Therefore, it does not seem appropriate to compare insect communities relative to the absolute time the carrion was exposed (e.g. Topp et al. 1982). If the decaying process is fast enough, a classification using clearly separated microserial stages better reflects the community structure.

Problems arise when successional stages of decay are used for a classification, because of the subjective criteria necessary for their definition, such as odour, shape, and degree of disintegration. This obstacle becomes obvious by comparing the variety of classifications proposed in the literature, ranging from 3 to 6 different stages of decay (e.g. Fuller 1934; Payne and King 1970).

Detailed observations on the feeding habits of carnivorous beetles gave further criteria for ecological separation in this group. The analysis of predator-prey relationships in carrion insects was simplified, because the predominant prey are blow fly maggots. The predator's body size and therewith the width of spread mandibles seem to be well correlated with the preferred maggot size. However, hister beetles, which are of small size and have a small width of spread mandibles, are able to overwhelm fully grown maggots. This might be due to a different function and morphology of the pincer-like mandibles. On the other hand, Philonthus and Creophilus exhibit significant differences in mandible size with respect to sex, which should not be interpreted as a differential use of food by males and females, but may be a secondary sex characteristic used in interspecific aggression and mating (Jepson 1984; Peschke, unpubl.).

The size of blow fly maggots is related to the successional stage, because the larvae develop fast and synchronously. Therefore, it also seems to be appropriate to use the development of blow flies as a scale along the time axis (deposition of eggs, occurrence of consecutive size classes of maggots, emigration of maggots, pupation). The emigration of maggots is the most important successional mark for the community: saprophageous beetles and their larvae become predominant and the set of predators has remarkably changed.

Blow fly development also affects the spatial microhabitat structure at a carcass. Various predaceous and parasitoid insects successively encounter their prey or hosts on the upper surface, where the fly eggs had been deposited, in the cavities within the corpse or the soil underneath (medium sized maggots), in the periphery of the corpse to feed on the last instar larvae, or in the carrions' surroundings to prey on migrating

maggots. In this case, the temporal succession also reflects the spatial gradient of microhabitats.

Broad niche overlaps have been observed among some of these carrion insects after separation along successional and microhabitat gradients. On the other hand, we also described several examples of ecological separation of these species by their differential abundances in macrohabitats and seasons. However, in respect to these niche dimensions our investigations remain incomplete, since many species with a low abundance have been neglected by the method of handling living insects, which had been choosen for direct observation of feeding habits. Detailed investigations of selected taxa have been reported in the literature (Staphylinidae: TOPP 1982; Silphidae: ANDERSON 1982; *Necrophorus*: WILSON et al. 1984).

Some carnivorous insects of the carrion insect community are not restricted to carcasses only. HANSKI and KOSKELA (1977) and TOPP et al. (1982) already discussed the problem of habitat specialists and generalists in their studies on dung inhabiting beetles or carrion rove beetles, respectively. These terms should be used with caution, since we found some species *(Philonthus)* which were generalists with respect to habitat, and on the other hand, specialists concerning prey (maggots of distinct size). Additionally, they reduce the number of maggots considerably. In contrast, specialists in respect to habitat *(Thanatophilus)* may be generalists concerning their nutrition (maggots as well as decaying meat). Especially, it seems not to be appropriate to characterize large taxons like the Staphylinidae as habitat generalists (e.g. TOPP 1982), as long as very abundant species like *A. curtula* turn out to be extreme carrion specialists.

4.2. Functional relationships

The evidence of ecological separation centers on the question, to what extent might competition have been the selective factor for this separation. Resource partitioning among blow fly maggots has been intensively investigated (DENNO and COTHRAN 1975; HANSKI and KUUSELA 1977; HANSKI 1976; BEAVER 1977; KUUSELA 1983, 1984; KNEIDEL 1983, 1984; JOSWIG 1985). We could also demonstrate the effect of scramble competition by manipulating food quantities.

In order to evaluate the competition among carnivorous carrion beetles, one has to demonstrate that the blow fly maggots are in fact a limited resource. The maggots are the dominant primary consumers of carrion, assimilating most of the decaying meat (PUTMAN 1977, 1978). The predators, however, remove a considerable number of these maggots. Additionally, maggots which have the proper size for certain predators are only present for a short period of time. The availability of maggots as prey may also be reduced by their behaviour. They are densely packed in carrion cavities and emit a strong ammoniac stench. Predaceous beetles could not be observed in these concetrated bulks and only fed on maggots which were located in the periphery.

Predation reduced maggot numbers, but also lessened their competition for food, which resulted in a higher weight of postfeeding maggots or puparia. NICHOLSON (1950) has shown that a higher weight of maggots causes a higher rate of pupation. Additionally, larger females hatching from large puparia are much more fecund than small ones. We therefore assume that the negative effect of predators on maggot numbers is com-

pensated by the developmental flexibility of the blow flies regulating the total reproductive success: A large number of small puparia results out of a low level of predation.
· Many flies hatch, but per female only a small number of offspring will be produced. When predation was highly effective, a small number of large puparia developed. Each
· of the few resulting females, however, will have a large number of offspring.

In the first instance, the developmental flexibility of blow flies seems to be an adaptation to the variable degree of competition due to stochastic processes in deposition of blow fly eggs (KUUSELA 1983). However, we also observed an extreme variability in the abundance of predators regulating the maggot population and thereby the degree of competition between blow fly larvae. TOPP (1982) already stated a remarkable variation in the number of individuals, and in the diversity of carrion inhabiting rove beetles at carcasses simultaneously exposed in the same area.

The early colonization and the rapid development of blow flies may be a result of the r-selected life cycle strategy, the competition among the larvae, and probably the competition with microorganisms. As an additional effect, the maggots also evade predation and parasition through a fast development. Finally, migration and dispersal of postfeeding blow fly larvae to the carrions' surroundings seems to be a mechanism to avoid further predation and parasitation

4.3. Limiting resources

We hitherto postulated that distribution along axes of various niche dimensions is a measure for partitioning the food resources. We have to discuss now, how far other resources might also be relevant for the description of the niche hyperspace. Therefore, detailed information on the autecology of each species seems to be necessary. We restricted our investigation to a case study on the ecology and behaviour of the rove beetle, *Aleochara curtala.*

Availability of carcasses. The localization of a corpse is the first critical phase in the life cycle of carrion insects (dispersal strategies: SHUBEK 1968; BEAVER 1977; McKINNERNEY 1978; TOPP et al. 1982). However, populating a carcass does not solely guarantee reproductive success, because vertebrate scavengers or burying *Necrophorus* beetles may remove the carcass very soon. For *A. curtula*, the carcass in itself is not the limited resource, but the availability of blow fly pupae serving as hosts for the larvae, which is determined through the persistence of the carcass during the whole process of decay.

Food for adults. The quantity and quality of food affects both sexes in different ways. Females feeding on maggots lay more eggs than those only provided with decaying meat (PESCHKE et al. 1987a). Males also feed on maggots if available, however, maggots are not necessary for a successful reproduction (PESCHKE, unpubl.). Migrating individuals need food in intervals of at least 5 d. They also populate carcasses after emigration of maggots, where the main food resource seems to be decaying meat. This allows searching for another carrion more favourable for reproduction (PESCHKE, unpubl.). Thus, we did not observe an overall dependence of a species on a certain food quality, but we have to consider sensitive stages (MÜLLER 1983, 1986), for which certain food qualities are in fact a limiting resource.

Prey and hosts for larvae. HANSKI and KOSKELA (1977) already concluded from their exemplary study on resource partitioning of dung inhabitating beetles that the inter-

pretation of the species community might be quite different, if the ecology of the larval stages is considered, too. However, for most of the involved species the larval biology is unknown. In the carrion insect community, the adults of the most abundant predators of medium size (A. curtula, H. cadaverinus, P. politus) are very similar with respect to nutrition and to their abundance in successional stages, microhabitats, and seasons. Their larvae, however, exhibit quite different life habits: Those of Aleochara are parasitoids of blow fly pupae (PESCHKE and FULDNER 1977), Hister larvae are predators on puparia (LINDNER 1967), and larvae of Philonthus probably prey on a variety of small arthropods (EGHTEDAR 1970; LIPKOW 1982).

The reproductive success of A. curtula is limited by the availability of Lucilia pupae as hosts for the parasitoid larvae. Due to the fast and synchronous development of blow flies, the parasitoids can only find puparia of optimal age for their development in a restricted period of time during the succession. Additionally, the location of host puparia varies due to the migration of maggots. Weather changes may strongly influence the availability of hosts. Finding a single carcass is not a guarantee for reproductive success. We estimate that only 2% of the first instar larvae complete their development and that only 30% of the females gain reproductive success (2 larvae/female). We calculated these data from the average egg rate (PESCHKE et al. 1987a), the number of females visiting the carcass during the critical stage (recapture experiments), and from the percentage of parasitized pupae. We also observed carcasses with a high abundance of A. curtula adults but without any resulting parasitation of blow fly pupae (rainy periods in 1980, PESCHKE, unpubl.). Longevity and the capability of settling several carcasses subsequently are adaptations to the unpredictable reproductive success. Behavioural and developmental adaptations of host searching larvae and egg laying females ensure temporal and spatial coincidence with hosts (PESCHKE et al. 1987a. b); and larvae were shown to minimize competition among each other (FULDNER et al. in prep.).

Site of egg deposition and mating. Females of A. curtula deposit their eggs in the surroundings of carcasses in order to make it easier for larvae to find hosts. This behaviour causes the different abundances of sexes in the various microhabitats: The females migrate from the core of the carcass, where they shortly stay to feed and copulate, to the periphery for egg laying. After the period where hosts had the optimal age has ended, females only visit a carcass briefly. The resulting male bias of the sex ratio of A. curtula is only observed during the reproductive season.

Copulations of A. curtula were mainly observed directly at the carcass, which is the mating site with the highest probability for males to encounter females. The females are detected at close range by pheromones (PESCHKE 1978b, 1983, 1986; PESCHKE and METZLER 1987). The male biased sex ratio causes violent competition among males for females which are the limited resource (PESCHKE 1985a, b). The males stay at the carcass for a much longer period than females and thus enhance their chance to copulate with females passing through the carcass.

Thus, the distribution of A. curtula in various temporal and spatial resource gradients does not only reflect the special use of the food resource within the carrion insect community, but also the differential requirements of sexes for food as well as for sites for mating and egg deposition. The parasitoid life habit of the larvae seems to be

the bottleneck in the development of the species affecting the behaviour of adults and their reproductive success. In general, more autecological data on other species are necessary to better understand the carrion insect community.

5. Zusammenfassung

Ökologische Sonderung, funktionelle Beziehungen und limitierende Ressourcen in einer Artengemeinschaft von Aasinsekten

An Kaninchenkadavern wurde die ökologische Sonderung von 19 häufigen Aasinsektenarten (Imagines und z. T. Larven) unter Berücksichtigung von 4 Nischendimensionen untersucht. Bei den (1.) Makrohabitaten (Wald-Schonung) wurde besonders die Verteilung saprophager Käferlarven, bei der (2.) Saisonalität das unterschiedliche Vorkommen von Schmeißfliegen berücksichtigt. (3.) Die Stadien der Kadaverzersetzung wurden mit der temperaturabhängigen Entwicklung der Schmeißfliegen korreliert, die das zeitliche Vorkommen konkurrierender saprophager Käfer beeinflussen. Außerdem sind manche Räuber auf Maden bestimmter Größe angewiesen. Bei der Betrachtung von (4.) Mikrohabitaten (räumliche Untergliederung des Kadavers) konnten Arten ähnlicher Nahrungsnutzung in einem Nischenüberlappungsdendrogramm gruppiert werden.

Der quantitative Effekt von räuberischen Käfern auf die Fliegenmaden wurde in Freiland- und Laborexperimenten untersucht. Der Räubereinfluß bewirkt zwar eine Reduktion der Zahl sich entwickelnder Maden, diese erreichen aber bei verminderter Konkurrenz ein höheres Puppengewicht. Der Reproduktionserfolg der Schmeißfliegen ist somit durch die Flexibilität der Madenentwicklung ausgeglichen. Weiterhin wurde der Einfluß von Räubern und Parasitoiden auf die Puppen von Schmeißfliegen quantifiziert.

In einer Fallstudie am Kurzflügler *Aleochara curtula* wurden die unterschiedlichen Abundanzen von Männchen und Weibchen untersucht. Das Geschlechtsverhältnis der am Kadaver frisch eintreffenden Käfer ist zunächst ausgeglichen, die Käfer fressen und kopulieren. Die Weibchen verlassen das Aas zur Eiablage früher als die Männchen, wodurch das Geschlechterverhältnis stark verschoben wird. Die Weibchen legen im Kadaverumfeld die Eier, und die parasitoiden Eilarven suchen nach verstreuten Fliegenpuparien als Wirten. Die zeitliche und räumliche Verteilung von Männchen und Weibchen ist also nicht nur vom Nahrungsbedarf der Imagines abhängig, sondern auch von anderen limitierenden Ressourcen, wie den Plätzen für Partnersuche und Eiablage und den Wirten für die Larven.

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