Zool. Jb. Syst. 121 (1994), 171-192
Gustav Fischer Verlag Jena

Biologisches Institut I (Zoologie) der Albert-Ludwigs-Universitat Freiburg,
Freiburg, Deutschland

Resource Partitioning in Coprophagous Beetles from Sheep Dung: Phenology and Microhabitat Preferences

PETER SOWIG and THOMAS WASSMER

With 6 Figures

Abstract

On a pasture in SW-Germany coprophagous beetles (Scarabaeidae, Hydrophilidae: Sphaeridiinae and Staphylinidae: Oxytelinae) from sheep droppings were studied considering the following niche dimensions: season, size, type and water content of the dropping.

1. Phenological differences were found especially within endocoprid Scarabaeidae. Dominant *Aphodius-species.* were clearly separated from each other by their phenology, while nearly all Hydrophilidae from the genus *Cercyon* and paracoprid Scarabaeidae were most abundant in May.

2. Sheep produce different types of droppings, either compact lumps or small pellets. The latter are mostly deposited in groups. Since these pellets dry out quickly, but rehydrate during rainfall, a high variability of humidity conditions makes pellets unattractive to many dung bettles.

3. Pairwise niche overlap indices in coprophagous beetles from sheep droppings were calculated regarding two niche dimensions: dropping size and water content. Cluster trees showed a clear distinction between species according to these microhabitat factors. Especially Hydrophilidae tend to avoid small droppings which might be due to unstable humidity conditions there. Mean intrageneric overlap within genera with more than one species was equal to or even higher than mean intergeneric overlap rates.

1. Introduction

Resource utilization of cooccuring species within one biotope should differ by a limiting similarity according to the competitive exclusion principle (GAUSE 1934). This limiting similarity should lead to a limited number of species and a limitation of diversity within one community. Contradictory to this stands the question "Why are there so many kinds of animals?" (HUTCHINSON 1959). Especially in invertebrate taxa like insects with high numbers of species competitive exclusion seems to be less evident. Thus, the validity of GAUSE'S principle and thereupon the existence of competition has been discussed quite controversially (DEN BOER 1980, 1986; ABRAMS et al. 1986). Many studies focussed on additional explanations of the coexistence of competing similar species like high intraspecific interference competition (VANCE 1985), intraspecific aggregation (ATKINSON and SHORROCKS 1981), the role of predation on stable coexistence (CASWELL 1978, CONNELL 1971), and chance events (review by HARVEY and SILVERTOWN 1983). High diversities in case of communities of insects and other taxa of small invertebrates with high numbers of species are said to be due to spatio-temporal heterogeneity of ephemeral microhabitats ("patchy environment"), since unstable conditions may permit ecologically similar species to coexist (HORN and MACARTHUR 1972, HANSKI 1983, SHORROCKS 1990). Their theoretical models showed, that migration between and local extinction within insular patches leads to a possible coexistence of even quite similar species. One goal of community ecology is to detect, which resources are partitioned by coexisting species, and how far these species are separated in niche space. This may help us to explain the extreme species richness of insect communities.

Since the last decades excrements from large herbivores were studied by many ecologists in order to detect interactions of species within such a patchy environment (ADAM 1986, BREYMEYER 1974, HANSKI and KOSKELA 1979, HOLTER 1982, LANDIN 1961, LUMARET and KIRK 1987; MADLE 1934, MOHR 1943, NEALIS 1977, OTRONEN and HANSKI 1983, RAINIO 1966, STEVENSON and DINDAL 1985). Since from a chosen faeces all insects can be extracted completely, the composition of this community can be documented accurately, which makes dung pats well suited for studies of patterns of resource partitioning. Dung is used as both microhabitat and food resource by a variety of beetle and fly species acting as coprophagous decomposers or carnivorous predators. While most previous papers were confined to Scarabaeidae as dung beetles "sensu strictu", this study focusses on coprophagous beetles from the following taxonomic groups: Scarabaeidae: Geotrupinae, Aphodiinae and Onthophaginae; Hydrophilidae: Sphaeridiinae; Staphylinidae: Oxytelinae. Coprophagous Scarabaeidae feed on dung as larvae and as imagines, while Sphaeridiinae are coprophagous only as adults. Oxytelinae are not strongly restricted to dung and use other decaying substrates, too. Within the Scarabaeidae, eggs from Aphodiinae are laid directly in the dung pat ("endocoprid"), while members of Geotrupinae and Onthophaginae build brood chambers beneath the pat and provide them with dung ("paracoprid") to avoid desiccation (BURMEISTER 1930).

Dung pats can be considered as discrete patches with a certain combination of characters like age, size or water content. If these characters influence a species-specific patch choice by dung beetles, species compositions between patches should be different. While most ecological work has been done with cow dung (review by HANSKI 1990), faeces from sheep were considered only in a few studies (LANDIN 1961, BREYMEYER 1974, OLECHOWICZ 1974, ADAM 1986, LUMARET and KIRK 1987). One quite obvious feature of sheep dung is that sheep produce two different types of droppings: 1. compact lumps, which vary widely in size, or 2. small pellets, which are deposited in groups or isolated as single pellets. In contrast to cow dung, which develops a compact crust on its surface, sheep droppings are able to rehydrate by dew or during rainfall. Thus, especially in small droppings, water content varies widely and can neither be correlated with its age (LANDIN 1961, LUMARET and KIRK 1987) nor with its size. Therefore, water content and dropping size can be considered as important microhabitat factors for patch choice, while exposition time (= age) does not seem to be a good parameter in the control of succession of insect communities in sheep droppings. As patch size varies extremely in sheep droppings, it might play an important role in niche separation. In a tropical forest PECK and HOWDEN (1984) used pitfall traps with dung baits of different size and showed, that in fact dung size can be regarded as a niche dimension for dung beetles.

Previous studies on the community structure of dung feeding beetles focussed mostly on phenology (LUMARET and KIRK 1987), macrohabitat preferences (LANDIN 1961, NEALIS 1977), succession (HANSKI 1980a), and brood care strategies (BRUSSAARD 1983, BURMEISTER 1930, DOUBE 1990, HALFFTER and MATTHEWS 1966, KLEMPERER 1983). A common method in experimental dung beetle ecology is to exclude the influence of patch size by exposing standardized cow dung pats of equal weight in the field (HANSKI and KOSKELA 1977, HOLTER 1982, OTRONEN and HANSKI 1983, RAINIO 1966). This paper examines the extent to which coprophagous beetles inhabiting sheep dung are separated from each other in four niche dimensions: season, type of dropping, dropping size, and water content.

2. Material and Methods

2.1. Field work and getting raw data

We selected two adjacent study sites at 400 m above sea level in a 65 ha large area near Freiburg (Southwest-Germany) which was used extensively as a sheep pasture at least during the last two decades. For a detailed description of this locality see WASSMER and SOWIG (1993). During our study period in 1990, sheep were present only in spring (April and May) and autumn (September - November). Once in these months we randomly collected sheep droppings of different size and water content between 9:00 and 12:00 GMT. We yield a total of 698 sheep droppings with a dry weight of 10.67 kg as a whole.

A small piece from each collected dropping was weighted, and dried in an incubator until weight was constant to obtain its water content. From the fresh weight of the whole dropping and its water content the dry weight was computed as a measure of dropping size. Fresh weight proved to be an unsuitable measure of dropping size, since its water content varied between 18.5 and 86.6%. From each dropping the following factors are considered in this study: month, size measured as dry weight, water content in % and dropping type (lump, pellet group or single pellet). The flotation method (MOORE 1954) was used to extract the beetles from the dung. All dung feeding beetles were identified.

2.2. Presentation of phenologies

In order to detect seasonal differences in community structure, individuals from all collected droppings of each month were lumped together. We regarded this sample as representative for the whole community and described its structure by SHANNON'S index of diversity and evenness (Table 1). Since amounts of collected dung were not exactly equal in each month and the abundances of species tended to decrease with their body size, abundances were converted to mg dry biomass per g dung dry weight (called "relative biomass" in the following text) to compare phenological data directly between species. Dry weight of each species was measured from 20 collected individuals of the more common species, or weight measurements were taken from LUMARET and KIRK (1987) and HANSKI and KOSKELA (1979).

2.3. Niche metrics

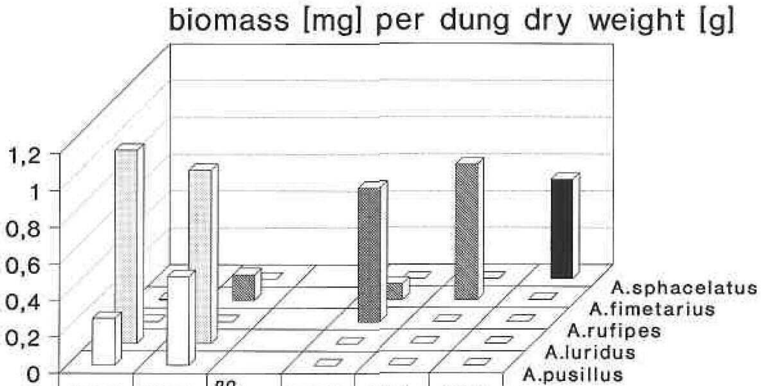
For reasons explained below, data from spring and autumn were analysed separately from each other. Each set of raw data (lists of species abundances in each collected faeces) was condensed to two resource matrices with three resource states (classes) regarding the two niche dimensions dung dry weight and water content respectively. Ranges of classes were set in such a way that samples from each class constituted roughly equal total dung dry weights (see column 3 in Tab. 3). We admit that lower and upper boundaries in the medium class of each matrix lie close together, but his method guarantees: 1. all resource states are represented equally, 2. limits are set by no means subjectively and 3. as each resource state "offers" equal total amounts of dung to the dung beetles, productivity should not differ between the resource classes. As pointed out by HANSKI (1978) and recently by LOREAU (1990), equality of productivities in all resource states is a basic requirement to compute the following niche metrics. HANSKI (1978) indirectly deduced productivity of resource states from their numbers of inhabiting individuals. This procedure seems to be justifiable if a species community has been considered as a whole. As our study is restricted to guilds of dung feeding beetles, total individual numbers may be influenced not only by productivity but by predation or parasites, too. Further, since mg biomass dung beetles/g dung varies from month to month (Tab. 1), a certain amount of dung would refer to different productivity depending on month. In this study we assume that with respect to coprophagous beetles productivity of each resource state better correlates with its total amounts of dung. Nevertheless we admit that finally the availability of a resource, which is not necessarily equal to its amount but more difficult to investigate, would be the best measure of productivity.

Since species with low abundances tended to be distributed randomly to resource classes, we excluded all species with less than five individuals from the analyses. Resource partitioning regarding the two microhabitat factors dry weight and water content separately was computed as pairwise niche overlap measured as realtive mutual information according to eq. 24 in COLWELL and FUTUYMA (1971). Following these authors the resource states were weighted with "relative weighting factors" (eq. 18). Pairwise overlaps were presented as WPGMA-Clusters (weighted pair-group method using arithmetic averages, SNEATH and SOKAL 1973), because this method better reveals distances between clusters of different size (LEGENDRE nd LEGENDRE 1983). HANSKI's (1978) weighting method of resource states led to very similar cluster trees, which are not presented here. The cluster trees were used to group together species with similar resource requirements. All species within the same group were distributed similarly in the resource matrix. Therefore *Aphodius paykulli*, for instance, was arranged to group 1 in Figure 4, but *Oxytelus sculpturatus* was excluded from group 2, although niche overlap between *O. sculpturatus* and the rest of group 2 was somewhat broader than between *A. paykulli* and the rest of group 1.

To analyse the distribution of congeneric species along one niche axis we asked whether mean pairwise overlap between species within one genus differed from mean pairwise overlap with members of the other genera or not. Since values of overlap were by no means distributed normally MANN-WHITNEY'S U-Test was used to prove the significance of the observed differences (Tab. 4).

3. Results

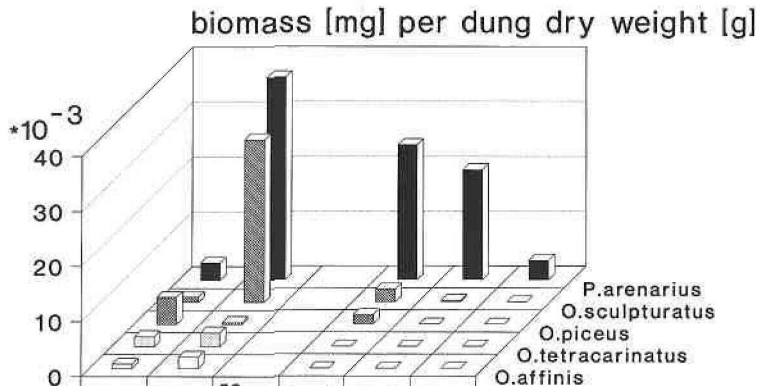
We obtained 5915 individuals from 43 dung feeding beetle species which we split up to 4 "guilds": 5 paracoprid Scarabaeids, 17 endocoprid Scarabaeids, 14 Hydrophilids (Sphaeridiinae), and 7 copro- and detritophagous Staphylinids (Oxytelinae). The complete list of species and abundances is given by WASSMER and SOWIG (1993).



	April	May	no sheep	Sept.	Oct.	Nov.
A.sphacelatus	0,015	0		0	0,002	0,54
A.fimetarius	0,006	0,142		0,092	0,74	0,005
A.rufipes	0	0		0,734	0	0
A.luridus	1,058	0,95		0	0	0
A.pusillus	0,259	0,492		0	0	0

Fig. 1. Phenology of the five most common *Aphodius-species.* Not abundances but mg biomass per g dung dry weight were used to compare all values directly.

No striking differences in the phenologies within Hydrophilidae were found, since 10 from 14 species reached their maximal abundance in April or May. Most paracoprid Scarabaeidae were too rare (378 individuals in total, most of them belonged to *Onthophagus ovatus),* to describe their phenology.



	April	May	no sheep	Sept.	Oct.	Nov.
P.arenarius	3,2	37		24,7	20,1	3,6
O.sculpturatus	1	29,7		2,3	0,3	0
O.piceus	4,9	0,4		1,7	0	0
O.tetracarinatus	1,8	2,5		0	0	0
O.affinis	0,8	2,1		0	0	0

Fig. 2. Phenology of the five most common Oxytelinae-species analogous to Fig. 1.

Table 2. Numbers of species which occur in spring only, in spring and autumn, and autumn only.

guild	spring only	spring and autumn	autumn only
paracoprid Scarabaeidae		3	2
endocoprid Scarabaeidae	7	5	5
Hydrophilidae (Sphaeridiinae)		12	2
Staphylinidae (Oxytelinae)	3	4	–
total	10	24	9

Table 3. Resource classes of the niche dimensions dropping dry weights and water content.

limits of resource-classes	number of samples	sum of dung dry-weights	number of species	number of individuals	relative resource-weightening after . . .	
					COLWELL and FUTUYMA (1971)	HANSKI (1979)
niche dimension: droppingg dry weight						
• season: spring						
0- 10.49 g	163	962.8 g	25	1511	0.315	0.324
10.5-17.25 g	71	962.0 g	32	1119	0.180	0.251
> 17.25 g	31	962.0 g	28	1856	0.505	0.424
• season: autumn						
0- 16.09 g	270	2570.6 g	23	451	0.425	0.450
16.1-34.9 g	113	2611.7 g	24	470	0.125	0.127
>35 g	50	2610.7 g	23	508	0.450	0.423
niche dimension: dropping water content						
• season: spring						
0-76.39%	114	965.5 g	26	997	0.427	0.563
76.4-78.6%	73	951.0 g	30	1940	0.286	0.194
>78.6%	78	969.9 g	30	1549	0.287	0.243
• season: autumn						
0-73.09%	173	2591.5 g	23	421	0.309	0.352
73.1-77.9%	127	2636.7 g	28	439	0.272	0.297
>77.9%	133	2574.8 g	19	569	0.418	0.352

In summary, there was an extreme difference in species compostion between spring and autumn. Ten of the 43 species were present in spring only and 9 in autumn only (Tab. 2). This and the absence of sheep for three months during summer led us to the decision to analyse the influence of microhabitat factors (dropping size and water content) in spring and autumn separately.

3.2. Separation by dropping weight

The upper part of table 3 shows the limits of three classes of dung dry weight in spring and autumn. Five species groups can be readily distinguished in spring (Fig. 3). The Scarabaeid *Oxyomus sylvestris* and the Hydrophilid *Megasternum boletophagum* are restricted to the first two classes (small and medium-sized droppings). Species from group 2 are present in all classes, but there is a tendency to smaller droppings. Group 3 contains species, which are distributed nearly equally

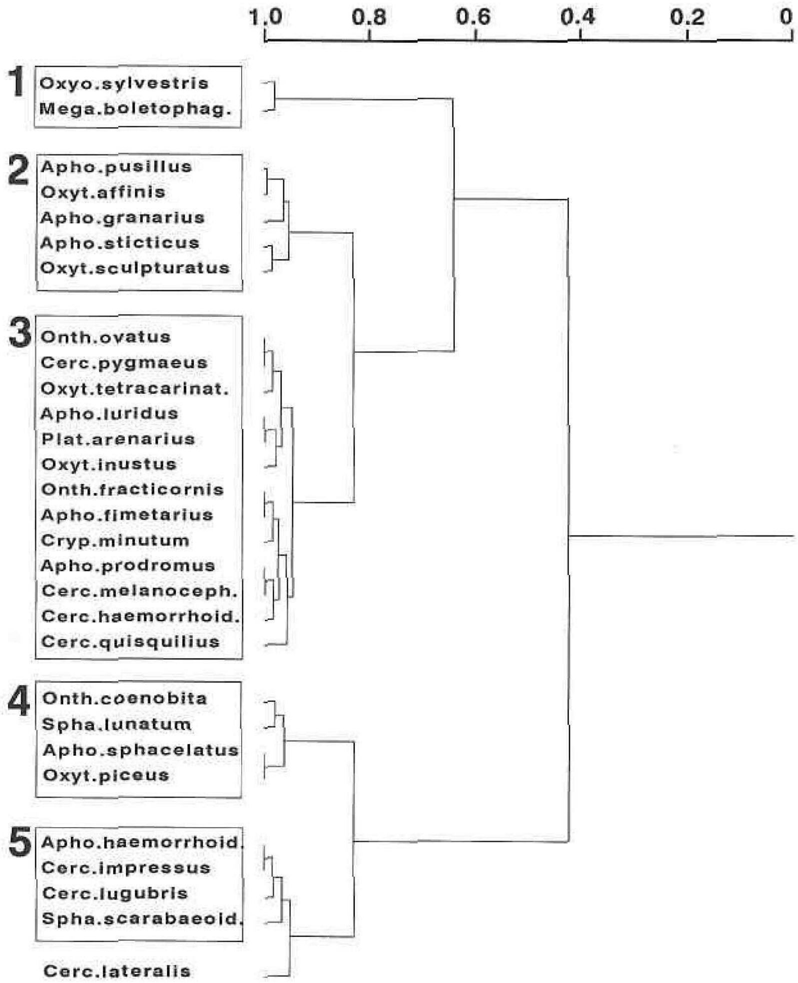


Fig. 3. WPGMA-cluster of dung beetles in spring regarding to dropping size.

Table 4. List of genera with more than one species. Mean pairwise overlap rates refer to resource classes defined in Table 3. It is tested, wether overlap within one genus differs from overlap with members of the other genera.

genus	number of species	mean overlap with species		significance of differences according MANN-WHITNEY's U-Test
		from the same genus	from the other genera	
dimension: dropping dry weight				
• season: spring				
Onthophagus	3	0.819	0.836	n.s.
Aphodius	8	0.844	0.821	n.s.
Sphaeridium	2	0.870	0.760	n.s.
Cercyon	7	0.901	0.806	$p < 0.01$
Oxytelus	5	0.840	0.817	n.s.
• season: autumn				
Onthophagus	3	0.917	0.625	$p < 0.005$
Aphodius	8	0.759	0.714	n.s.
Sphaeridium	2	0.949	0.599	$p < 0.05$
Cercyon	4	0.809	0.706	n.s.
Oxytelus	2	0.946	0.789	$p < 0.05$
dimension: dropping water content				
• season: spring				
Onthophagus	3	0.729	0.702	n.s.
Aphodius	8	0.785	0.810	n.s.
Sphaeridium	2	0.830	0.686	n.s.
Cercyon	7	0.951	0.846	$p < 0.001$
Oxytelus	5	0.825	0.817	n.s.
• season: autumn				
Onthophagus	3	0.859	0.671	$p < 0.05$
Aphodius	8	0.640	0.719	n.s.
Sphaeridium	2	0.722	0.708	n.s.
Cercyon	4	0.832	0.774	n.s.
Oxytelus	2	0.920	0.779	n.s.

3.3. Influence of excrement type

84 of 698 faecal droppings collected were single pellets or pellet groups. Their mean water content (+ standard deviation) was 71.3% ± 10.3, lumps were not significantly damper (73.1% + 11.9; MANN-WHITNEY'S U-Test: p = 0.09, n.s.). Mean dry weight was 14.8 g + 13.5 for pellet groups and 15.7 g + 14.2; (MANN-WHITNEYS U-Test: p = 0.04, n.s.) for lumps. On the assumption that pellets are as attractive as lumps and considering the relation between total masses of collected pellets and lumps (1 :9.431), one would except 572 of 5915 beetles to occur in pellets. However, only 318 individuals (2*2-contingency-table: $p < 0.001$) were collected from pellets. Table 5 contains the 21 species which were found in pellet groups

Table 5. List of 21 species occuring in pellets, too. A 2*2-table-test was performed for each species to defect differences from equal distribution between pellets and lumps. Only two species were significantly less frequent in pellets than in lumps. Species with "?" were too rare in pellets to perform a correct statistical test.

species	total abundances	abundance in single pellets or pellet groups	occurence in single pellets, too? (y/n)	significance
Scarabaeidae				
Onthophagus ovatus	335	39	y	n.s.
Onthophagus coenobita	11	1	n	?
Aphodius luridus	202	23	n	n.s.
Aphodius pusillus	602	64	n	n.s.
Aphodius biguttatus	3	2	n	?
Aphodius sticticus	103	14	n	n.s.
Aphodius sphacelatus	302	26	n	n.s.
Aphodius prodromus	50	2	y	?
Aphodius fimetarius	286	26	n	n.s.
Aphodius granarius	7	1	n	?
Scarabaeidae (total)	2171	198		n.s.
Hydrophilidae (Sphaeridiinae)				
Sphaeridium marginatum	3	1	n	?
Cercyon haemorrhoidalis	2391	59	y	$p < 0.0001$
Cercyon melanocephalus	57	3	n	?
Cercyon pygmaeus	162	4	n	?
Megasternum boletophagum	87	10	n	n.s.
Sphaeridiinae (total)	2906	77		$p < 0.0001$
Staphylinidae (Oxytelinae)				
Aploderus caelatus	8	1	n	?
Oxytelus piceus	25	1	n	?
Oxytelus sculpturatus	98	11	n	n.s.
Oxytelus affinis	102	5	n	n.s.
Oxytelus tetracarinatus	121	9	n	n.s.
Platystethus arenarius	476	16	y	$p < 0.0001$
Oxytelinae (total)	836	43		$p < 0.0004$

and/or single pellets. None of these species was significantly more frequent in pellets than expected, two of them were significantly rarer. Regarding species numbers 85.7% of Oxytelinae, 45.5% of Scarabaeidae but only 35.7% of Hydrophilidae were found in pellets.

3.4. Separation by water content

In the cluster tree from spring data, three distinct groups can be distinguished (Fig. 5). Group 1 unites species which prefer dryer droppings. Species from group 2 are distributed over all three classes, but tend to prefer damper droppings. Group 3

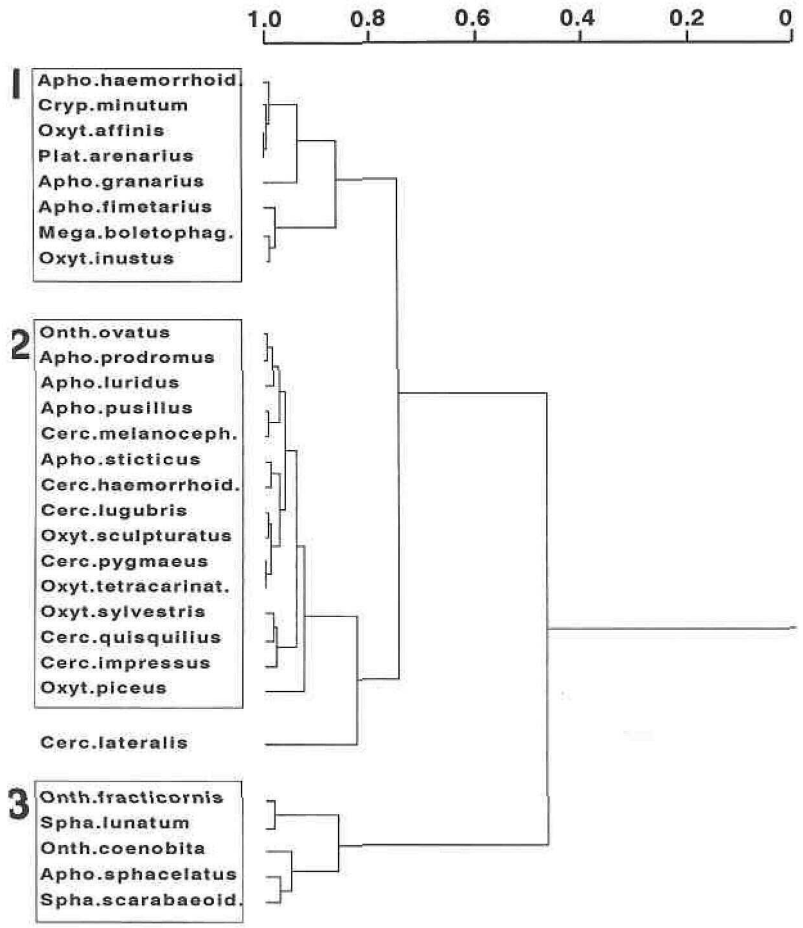


Fig. 5. WPGMA-cluster of dung bettles in spring regarding to water content.

contains species with strong preference for moist faeces. As in the niche dimension of dropping size, *Cercyon lateralis* fails to join any group again: 10 of the 16 individuals were found in medium-moist droppings.

The cluster from autumn data look quite different (Fig. 6): Group 1 contains species with strong preference for dry samples. They avoided damp droppings. Species from group 2 tend to prefer damp droppings, but also occur sparsely in dry droppings. Species from groups 3 and 4 reach their maximum in medium-moist droppings (second resource class). but species from group 3 were found rarely in dry droppings, while those from group 4 avoided damp ones. The Scarabaeids *Aphodius paykulli* and *A. sphacelatus* (group 5) were found nearly exclusively in damp droppings and are separated widely from all other species in the cluster tree. The Staphylinid *Aploderus caelatus* was found in 6 individuals only (2 in dry, 1 in medium and 3 in wet droppings).

Only in two cases (genus *Cercyon* in spring and genus *Onthophages* in autumn) overlap rates within one genus was significantly higher than overlap rates with other species. In the other genera no significant difference was found (Table 4).

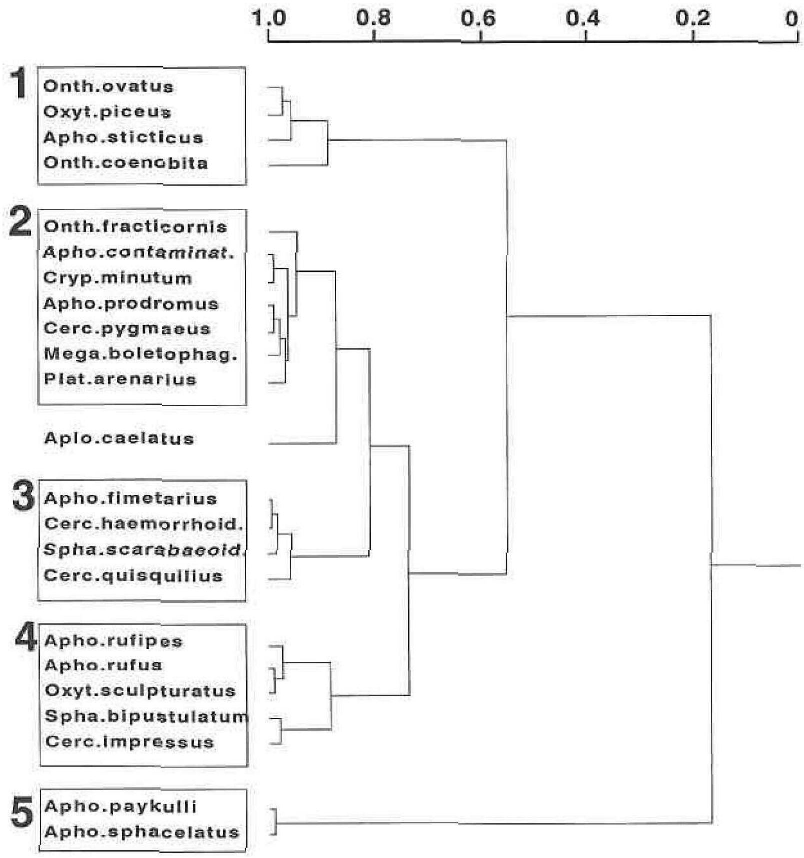


Fig. 6. WPGMA-cluster of dung beetles in autumn regarding to water content.

3.5. Separation by dropping size and water content together

All species, which were clustered together in the same group in both niche dimensions dropping size and water content (Figs. 3 and 5 resp 4 and 6), are listed in Table 6. How far are members of the same guild separated by these two niche dimensions? Paracoprid Scarabaeidae were never found in the same cluster in both dimensions. Each pairwise species combination within the endocoprid Scarabaeidae was congeneric, since in this guild 8 of 9 species with more than five individuals belonged to genus *Aphodius.* Combinations among Hydrophilids within the genus *Cercyon* occured in spring, while in autumn, species from different Hydrophilid genera were clustered together. In the Oxytelinae only *Platystethus arenarius* and *Oxytelus inustus* react similar to dropping weight and water content in spring.

It is remarkable, that the *Aphodius-species*, which react similarly to both niche dimenions never belong to the same subgenus. *Aphodius luridus* and *Aphodius prodromus* in spring have different phenologies. *A. luridus* is only active in spring, while *A. prodromus* occurs from autumn through winter to early spring. *Aphodius pusillus* and *A. sticticus* differ in phenology and habitat preferences. *A. sticticus* prefers pastures in the vicinity of woodland (LANDIN 1961). *Aphodius rufipes* and

Table 6. Which species are clustered by dropping size and water content to the same group? Species from the same genus are double framed, species from the same guild are single framed. Group numbers refer to figs. 3, 4, 5 and 6.

group number from niche dimension . . . dropping weight	. . . water content	Species
• season: spring		
2	1	*Aphodius granarius* *Oxytelus affinis*
2	2	*Aphodius pusillus* *Aphodius sticticus*
		Oxytelus sculpturatus
3	1	*Platystethus arenarius* *Oxytelus inustus*
		Aphodius fimeta rius *Cryptopleurum minutum*
3	2	*Onthophagus ovatus* *Oxytelus tetracarinatus*
		Cercyon pygmaeus *Cercyon melanocephalus* *Cercyon haemorrhoidalis* *Cercyon quisquilius*
		Aphodius luridus *Aphodius prodromus*
4	3	*Onthophagus coenobita* *Sphaeridium lunatum* *Aphodius sphacelatus*
• season: autumn		
1	1	*Aphodius sticticus* *Onthophagus coenobita*
1	2	*Onthophagus fracticornis* *Aphodius contaminatus*
2	1	*Onthophagus ovatus* *Oxytelus piceus*
2	2	*Megasternum boletophagum* *Cercyon pygmaeus*
		Aphodius prodromus
3	3	*Aphodius fimetarius* *Cercyon haemorrhoidalis*
3	4	*Aphodius rufipes* *Aphodius rufus*
4	3	*Sphaeridium scarabaeoides* *Cercyon quisquilius*
4	4	*Sphaeridium bipustulatum* *Cercyon impressus*

A. rufus differ in their body size, the first mentioned species is more than four times heavier. *Cercyon-species* mostly cooccur together in both niche dimensions in spring, since nearly all species tend to inhabit large damp droppings.

4. Discussion

How far is a community with 43 coprophagous beetle species representative in comparison with other studies? Unfortunately most previous papers in dung beetles dealt with Scarabaeidae only. In the vicinity of our study area only one other study on this item was conducted so far by GEIS (1981), who monitored occurrence of Scarabaeid-species on a sheep/cow pasture near Schelingen (Kaiserstuhl; SW-Germany) for many years. He recorded 35 Scarabaeid species, 65.7% of them were endocoprid. Our short-term study yielded 22 (77.3% endocoprid) Scarabaeid-species. Both study sites can be geographically arranged in a latitudinal gradient: In the Sierra Nevada (Spain) AVILA and PASCUAL (1988) recorded 53 Scarabaeid species, 54.7% were endocoprid. In Southern France 98 (only 51% endocoprid) Scarabaeid-species were studied by LUMARET and KIRK (1978) in different habitats. In southern Finland a dung beetle community investigated by HANSKI and KOSKELA (1977) contained only 19 Scarabaeid species, which were all andocoprid with exception *ofGeotmpes stercorosus.* Advancing northward, paracoprid Scarabaeids, especially those from genus *Onthophagus*, become rarer. According to BISTROM et al. (1991) only four *Onthophagus-species* are recorded from Finland, but all of them are probably extinct during the last two decades. Regarding Sphaeridiinae and Oxytelinae species richness seems to be quite high in our community. HANSKI and KOSKELA (1977) found 15 Sphaeridiinae- and 9 Oxytelinae-species, SUDHAUS et al. (1988) recorded 11 Sphaeridiinae- and 4 Oxytelinae-species from cow dung near Berlin, DE GRAEF and DESIERE (1984) studied 12 Sphaeridiinae on a cattle pasture, and ADAM (1986) observed only 5 Sphaeridiinae and 7 Oxytelinae from sheep dung on a dry pasture in Hungary.

4.1. Phenology

The absence of sheep during summer prevented a complete phenological survey throughout the year. We assume, that this circumstance only slighty affected our study, since sheep droppings appeared to be quite unsuitable as microhabitats for dung beetles under warm and dry conditions. ADAM (1986) found a much lower diversity of dung feeding beetles in sheep droppings than in cow pats in dry pastures in Hungary during summer. Our results are in good agreement with those from HANSKI and KOSKELA (1979), who found a phenological separation within the genus *Aphodius,* but not in the Oxytelinae and the genus *Cercyon* (Hydrophilidae).

4.2. Excrement weight

It is not unexpected, that a large species, such as the endocoprid Scarabaeid *Aphodius rufipes* prefers large droppings. According to MADLE (1934), larval development of *Aphodius rufipes* depends on large amounts of dung from big herbivores such as cows. We found third instar larvae from *Aphodius rufipes* in sheep dung, too. Thus, even this large species is able to reproduce in sheep droppings. PECK and HOWDEN (1984) compared numbers of dung beetles from pitfall traps with 200 ml dung baits to those with 2 ml dung baits. Beetles larger than 10 mm were found nearly exclusively in traps with 200 ml bait. More interestingly in our study, a preference for large droppings was by no means confined to large species. Especially Hydrophilidae tended to avoid small droppings, where humidity conditions are unstable.

The paracoprid Scarabaeidae (genus *Onthophagus)* behaved differently in spring and autumn: in spring, *Onthophagus coenobita* prefered large droppings, while *O. ovatus* and *O. fracticornis* behaved indifferently according to dropping size, but in autumn all these species mostly stayed in small droppings. This phenomenon can be explained by their brood care behaviour in spring: tunnelling the soil beneath a dung pat and provisioning brood chambers is profitable only under a large dung pat, which remains wet enough for several days and provides sufficient dung for many brood chambers. In autumn, when newly emerged beetles utilize dung for their own feeding requirements only, patch size seems to be less important for habitat selection.

While the benefits of large dung pats are evident, it seems not reasonable for a species to prefer small droppings. As listed in the upper part of Table 3; column 2, these small droppings are much more frequent than large droppings and can be discovered more easily by a randomly searching beetle. On the other hand olfactoric attraction of large dung pats may be higher. A species which does not strongly depend on large droppings will stay in any patch, even if it is small. But if interspecific competition in large dung pats becomes too high, an apparent preference for small droppings will be the result. In the above mentioned study by PECK and HOWDEN (1984) Scarabaeidae smaller than 10mm prefered small amounts of dung even when large species were excluded from the baits by a screen. Since in tropical forests desiccation might not play such an important role and, according to these authors, dung seems to be extremely scarce, these results can be compared with our study only cautiously.

In another context, influence of patch size on community structure has already been studied by one of us (SowiG 1989): the advantage of small flower patches to foraging bumble bees is a lower variance of amounts of nectar per flower. This facilitates the right decision of a foraging bumblebee, to stay or to leave a patch. Likewise from a dung beetle's point of view, small sheep droppings might be better to survey: the presence or absence of competitors, natural enemies or sexual partners can be detected much quicker. Thus, patch choise may perhaps more easily be optimized in small patches. We admit that this statement remains pure speculation, as long as results from detailed emigration experiments under standardized conditions (LANDIN 1961, YASUDA 1987) are mostly lacking.

Further we need more investigations on mechanisms of patch choise in different species of dung beetles as already done in other taxa: several experiments for instance with fish foraging in two artificial patches (at two feeding stations which dispensed different amounts of food) showed that poor patches were overused (review by MILINSKI 1988). This phenomenon can be explained either by limited abilities of foragers to recognize differences in patch quality, or by the fact that patch quality may change. The latter case forces each forager to change between patches to explore the actual distribution of patch profitabilities. Although more individuals tend to forage in rich than in poor patches, migration rate of occasionally exploring foragers is higher from rich to poor patches than vice versa.

4.3. Excrement type

Although not only large portions of dung are proved to be attractive to dung beetles, extremely small faeces like pellets are avoided, even if they lie close together in groups. Since many species of dung beetles obviously prefer compact excrement lumps to pellet groups of similar size, excrement type can be considered as another factor which influences habitat selection, Microclimatic conditions in different excrement types of sheep dung have been well examined by LUMARET and KIRK (1987) and confirmed by own investigations. Since the ratio of surface area to volume is larger in pellets than in lumps, pellets dry out more quickly than lumps. During rainfall however, pellets are able to rehydrate again. In our study Hydrophilidae and Staphylinidae in particular proved to be more sensitive than Scarabaeidae to these unpredictable changes in moisture conditions. The avoidance of sheep pellets was also observed by BURMEISTER (1930), who carried out preference tests with *Onthophagus nuchicornis* and *O. fracticornis* on cow pats, sheep lumps and sheep pellets. Both species refused to dig brood chambers under sheep pellets. But the small *Onthophagus emarginatus* however was observed to bury sheep pellets into the soil (LUMARET and KIRK 1987). AVILA etal. (1988) studied beetles feeding on rabbit droppings in Spain. They showed that a couple of species prefer these extreme small amounts of droppings.

4.4. Water content

In case of cow pats a crust prevents not only rapid desiccation but also soacking of the dung during rainfall. Thus, water content decreases continuously but slowly over time (LANDIN 1961). Succession of beetles and flies proceeds in quite regular patterns (MOHR 1943, HANSKI 1980a). As water content of sheep droppings varies due to rehydration, a progressive succession can be stopped or even reversed (LUMARET and KIRK 1987). Investigations are needed on how quickly different species react to changes in water content. Two strategies are possible: 1. a beetle can leave the dropping immediately after humidity conditions get worse. 2. a beetle can take a high variability of water content into account and remains in the dropping until conditions get better again. Beetles which tend to strategy 2 should be found in damp and dry droppings as well. Species from group 2 in fig. 5 and groups 3 and 4 in fig. 6 behaved in this way.

We found extreme differences between species, which led to distinct clusters regarding the resource states from Table 3. For instance, there is a remarkable difference between the closely related *A. prodromus* and *A. sphacelatus* in autumn. The occurrence of the latter species is confined to extreme damp droppings, while tolerance for drier droppings is higher in *A. prodromus.*

4.5. Intrageneric versus Intergeneric Overlap according to Dropping Weight and Water Content

One of the most important questions in community ecology is if and how far closely related (similar) species are separated along a niche axis. As explained above, according to CAUSE'S principle closely related species should not cooccur together. On the other hand congeneric species can react similarly to one factor due to physiological constraints. In our study some genera, particularly the scarabaeid genus *Aphodius* and the hydrophilid genus *Cercyon* were represented by several species. How are these congenerics distributed within one cluster tree?

Table 4 shows that mean overlap within one genus was either significantly higher or equal to mean overlap with members from other genera. A competitive exclusion of related species did not occur respecting the niche dimensions dropping weight or water content. Related species tend to react similarly especially to patch size. While four significant cases were observed according to dropping weight, only in two cases overlap between species within one genus differed significantly from overlap between other species according to water content (genus *Cercyon* in spring an genus *Onthophagus* in autumn). Our results are in good agreement with those from HANSKI (1991: p. 90) who tested distributions of pairwise spatial correlations from numbers of individuals from pitfall traps. As in our study he found no difference between the distributions of intrageneric and intergeneric correlations in case of genus *Aphodius*, but significantly higher percentages of higher correlations within the genera *Cercyon* and *Sphaeridium.* A missing competitive exclusion does by no means indicate missing competition. A certain ephemeral microhabitat may persist too short to allow a long struggle for existence between similar species. Changing conditions will favour this time one and next time another species. CODY (1973) concluded that character divergence appears neither at extreme high nor at extreme low abundances and predictabilities of resources.

When dropping weight and water content are regarded together as a two-dimensional niche space, species can be separated more clearly (Tab. 6). Nevertheless, some species still remain together in groups. *Aphodius-species* are separated better by their phenology or body size, since most of the 16 *Aphodius*-species from our study area were restricted to one or two months, and their body dry weights ranged between 0.7 mg *(Aphodius biguttatus)* and 32.8 mg *(A. rufipes).* There are many reports on severe interference competition among *Aphodius-larvae,* which use their strong mandibles to injure or to kill one another (MADLE 1934), and imaginal size in *Aphodius flmetarius* and *A.fossor* decreased with increasing population density in small amounts of dung (STEVENSON and DINDAL 1985). Therefore, differences in phenology and body size seem to be more suitable than microhabitat factors to avoid this kind of competition. A direct connection between body size and interference competition has been shown mostly in telecoprid (dung-ball rolling) Scarabaeidae (review by HANSKI and CAMBEFORT 1991).

Niche separation in Hydrophilidae and Staphylinidae remains less obvious. HANSKI and KOSKELA (1979) observed the same phenomenon and explained it by a smaller body size of most members of these families, since a given patchy environment is more coarse grained for smaller than for larger species. As higher heterogeneity can facilitate coexistence of similar species more easily (SLATKIN 1974, ATKINSON and SHORROCKS 1981), small species from the same genus are able to cooccur together within one habitat. Especially within the genus *Cercyon*, 4 species which behave similarly regarding microhabitat parameters, cooccur in spring. Only Hydrophilidae from genus *Sphaeridium* reach a body size comparable to Scarabaeidae. *Sphaeridium*-species colonize preferably fresh cow dung, and inhabit sheep droppings only exceptionally. In our study their abundances were insufficiently low for an extenstive interpretation.

4.6. Concluding remarks

Our surveys of sheep droppings can be considered as "snapshots" of a beetle community at a certain place and time. We know the exact abundance of each species in all examined faeces, but we can only conjecture the reason why a certain individual inhabits a certain patch. Not only foraging for food resources, but also reproductive strategies like mating, egg laying, and brood care behaviour may influence the decision to stay or to leave a patch. Only intensive studies on the biology of single species can lead us to a final understanding of the structure of dung communities.

5. Zusammenfassung

Auf einer Weide in SW-Deutschland wurden coprophage Kafer (Scarabaeidae, Hydrophilidae : Sphaeridiinae and Staphylinidae: Oxytelinae) aus Schafdung in Hinblick auf die Nischendimensionen Jahreszeit sowie GroBe, Typ und Wassergehalt des Exkrementes untersucht.

1. Phanologische Unterschiede wurden vor allem bei den endocopriden Scarabaeiden gefunden. Dominante *Aphodius-Arten* waren deutlich durch ihre Phanologie getrennt, wahrend fast alle Hydrophiliden der Gattung *Cercyon* und paracopride Scarabaeiden am haufigsten im Mai auftraten.

2. Schafe produzieren verschiedene Typen von Exkrementen: entweder kompakte Haufen oder kleine Pellets, wobei die letztgenannten meist in Gruppen abgesetzt werden. Da Pellets zwar schnell austrocknen, bei Regen jedoch wieder Wasser aufnehmen konnen, sind Pellets auf Grand dieser Schwankungen im Feuchtigkeitsgehalt unattraktiv fur viele Dungkafer.

3. Indices der paarweisen Nischeniiberlappung der Dungkafer wurden fur die Nischendimensionen GroBe und Wassergehalt der Exkremente berechnet. Clusterdiagramme zeigten eine klare Trennung zwischen den Arten bezuglich dieser Faktoren. Vor allem Hydrophiliden tendieren dazu, kleine Exkremente mit instabilen Feuchtigkeitsverhaltnisse zu meiden. Die durchschnittliche Nischeniiberlappung innerhalb einer Gattung mit mehr als einer Art war gleich oder sogar größer als die durchschnittliche Nischeniiberlappung zwischen Arten aus verschiedenen Gattungen.

Literature

ABRAMS, P. A., ROUGHGARDEN, I., GILLER, P. and P. J. DEN BOER : The competitive exclusion principle: Other views and a reply. Trends in Ecology and Evolution 1 (1986), 131 —133.

ADAM, L.: Beetles (Coleoptera) inhabeting sheep droppings in dry pastures of Hungary. Folia Entomologia Hungarica 47 (1986), 5 — 12.

ATKINSON, W. D. and B. SHORROCKS: Competition on a divided and ephemeral resource, a simulation model. Journal of Animal Ecology **50** (1981), 461—471.
AVILA, J. M. and F. PASCUAL: Contribucion al conocimineto de los escarabeidos coprofagos (Coleoptera, Scarabaeoidea) de Sierra Nevada: 3. Distribution altitutinal y temporal. Mus. Reg. Sci. Nat. Boll Torino 6 (1988), 217-240.
—, SANDOVAL, P., SCHMIDT, T. J. and F. SANCHEZ-PINERO: Contribucion al conocimiento de los Scarabaeidea (Coleoptera) coprofagos de los excrementos de conejo de la provincia de Granada (Espana). Elytron 2 (1988), 41-50.
BISTROM, O., SILFVERBERG, H. and I. RUTANEN: Abundance and distribution of coprophilous Histerini (Histeridae) and *Onthophagus* and *Aphodius* (Scarabaeidae) in Finland (Coleoptera). Entomologica Fennica 2 (1991), 53—66.
BREYMEYER, A.: Analysis of a sheep pasture ecosystem in the Pieniny mountains (the Carpatians). XL The role of coprophagous beetles (Coleoptera, Scarabaeidae) in the utilization of sheep dung. Ekologia Polska 22 (1974), 617-634.
BRUSSAARD, L.: Reproductive behaviour and development of the dung beetle *Typhaeus typhoeus* (Coleoptera, Geotrupidae). Tijdschrift voor Entomologie 126 (1983), 203—231.
BURMEISTER, F.: Die Brutfursorge und das Bauprinzip der Gattung *Onthophagus.* LATR. Zeitschrift fur Morphologie und Okologie der Tiere 16 (1930), 559—647.
CASWELL, H.: Predator-mediated coexistence: a non-equilibrium model. Am. Nat. 112 (1978), 127-154.
CODY, M. L.: Character convergence. Ann. Rev. Ecol. Syst. 4 (1973), 189-212.
COLWELL, R. K. and D. FUTUYMA: On the measurement of niche breadth and overlap. Ecology 52, (1971), 567-576.
CONNELL, J. H.: On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: Dynamics of Population (DEN BOER, P. J. and G. R. GRADWELL eds.) Proc. Advanced Study Inst. in Dynamics (1971) pp. 298-310.
DE GRAEF, F. and M. DESIERE: Ecologie des Coleopteres coprophiles en prairie permanente paturee. III. Dynamique et phenologie des guildes d'Hydrophilidae, de Scarabaeidae et de Geotrupidae. Bull. Soc. r. Sci. Liege 53 (1984), 158-172.
DEN BOER, L.: Exclusion or coexistance and the taxonomic or ecological relationship between species, Netherlands Journal of Zology **30** (1980), 278—306.
— The present status of the competitive exclusion principle. Trends in Ecology and Evolution, 1 (1986) 25-28.
DOUBE, B. M.: A functional classification for analysis of the structure of dung beetle assemblages. Ecological Entomology 15 (1990), 371-383.
GAUSE, G. F.: The struggle for existence. Baltimore 1934.
GEIS, K.-U.: Studien an der Lebensgemeinschaft der coprophagen Scarabaeiden (Coleoptera) im schutzwiirdigen Biotop der Schelinger Viehweide (Kaiserstuhl). Mitt. bad. Landesver. Naturkunde u. Naturschutz NF. 12 (1981), 275-303.
HALFFTER, G. and E. G. MATTHEWS: The natural history of dung beetles of the subfamiliy Scarabaeinae (Coleoptera, Scarabaeidae). Folia Entomol. Mexicana 12—14 (1966), 1-312.
HANSKI, L: Some comments on the measurements of niche metrics. Ecology 59 (1978). 168-174.
— Patterns of beetles succession in droppings. Ann. Zool. Fennici, 17 (1980a), 17—25.
— Spatial variation in the timing of the seasonal occurence in coprophagous beetles. Oikos 34, (1980b), 311-321.
— Coexistence of competitors in patchy environment. Ecology, 64 (1983), 493—500.
— Dung and carrion insects. In: Living in a patchy environment (SHORROCKS, B. and I. R. SWINGLAND, eds.) Oxford University Press (1990), 127-145.
— North temperate dung beetles. In: Dung beetle ecology (HANSKI, I. and Y. CAMBEFORT, eds) Princeton University Press (1991), 75—96.
— and CAMBEFORT, Y. (1991): Competition in dung beetles. In: Dung beetle ecology (HANSKI, I. and Y. CAMBEFORT, eds.) Princeton University Press (1991) 305—329.

— and KOSKELA, H.: Niche relations among dung-inhabiting beetles. Oecologia 28 (1977), 203-231
— Resource partitioning in six guilds of dung-inhabiting beetles (Coleoptera). Annales Entomologici Fennici 45 (1979), 1—12.
HARVEY, P. and J. SILVERTOWN: Can theoretical ecology keep a competitive edge? New Scientist (1983), 760-763.
HOLTER, R.: Resource utilization and local coexistence in a guild of Scarabaeid dung beetles *(Aphodius* sp). Oikos 9 (1982), 213-227.
HORN, H. S. and R. H. MACARTHUR: Competition among fugitive species in a harlequin environment. Ecology 53 (1972), 749-752.
HUTCHINSON, G. E.: Homage to Santa Rosalia or why are there so many kinds of animals? The American Naturalist 93 (1959), 146–159.
KLEMPERER, H. G.: The evolution of parental behaviour in Scarabaeidae (Coleoptera: Scarabaeidae): an experimental approach. Ecol. Ent. 1 (1983), 19—29.
EANDIN, B. O.: Ecological studies on dung-beetles (Col. Scarabaeidae). Opuscula Entomologica Supplement, 19 (1961), 1-227.
LEGENDRE, L. and P. LEGENDRE: Numerical Ecology. Amsterdam, Oxford, New York, 1983.
LOREAU, M.: The COLWELL-FUTUYMA method for measuring niche breadth and overlap: a critique. Oikos 58 (1990), 251-253.
LUMARET, J.-P. and A. KIRK: Ecology of dung beetles in the French Mediterranean region (Coleoptera: Scarabaeidae). Acta Zoologica Mexicana Nueva Seria 2 (1987), 41—55.
MADLE, H.: Zur Kenntnis der Morphologie, Okologie und Physiologie von *Aphodius rufipes* L. und einigen verwandten Arten. Zool. Jahrb. Anat. Onto. 58 (1934), 303—397.
MILINSKI, M.: Games fish play: making decisions as a social forager. Trends in Ecology and Evolution 3 (1988), 325-330.
MOHR, C. O.: Cattle droppings as ecological units. Ecological Monographs 13 (1943), 276-298.
MOORE, I.: An efficient method of collecting dung beetles. Pan-Pacific Entomologist 30 (1954), 208.
NEALIS, V. G.: Habitat associations and community analysis of South Texas dung beetles (Coleoptera: Scarabaeinae). Canad. J. Zool. 55 (1977), 138-147.
OLECHOWICZ, E.: Analysis of a sheep pasture ecosystem in the Pieniny mountains (the Carpathians). X. Sheep dung and the fauna colonizing it. Ekologia Polska 22 (1974), 589-616.
OTRONEN, M. and I. HANSKI: Movement patterns in *Sphaeridium:* Differences between species, sexes, and feeding and breeding individuals. Journal of Animal Ecology 52 (1983), 663-680.
PECK, S. B. and H. F. HOWDEN: Response of a dung beetle guild to different sizes of dung bait in a Panamanian rainforest. Biotropica 16 (1984), 235—238.
RAINIO, M.: Abundance and phenology of some coprophagous beetles in different kinds of dung. Annales Zoologici Fennici 3 (1966), 88—98.
SHORROCKS, B.: Coexistence in a patchy environment, in: Eiving in a patchy environment (SHORROCKS, B. and I. R. SWINGLAND, eds.). Oxford University Press (19990), 91—106.
SLATKIN, M.: Competition and reginal coexistence. Ecology 55 (1974), 128—134.
SNEATH, P. H. A. and R. R. SOKAL: Numerical Taxonomy. San Franzisco 1973.
SOWIG, P.: Effects of flowering plant's patch size on species composition of pollinator communities, foraging strategies, and resource partitioning in bumblebees (Hymenoptera: Apidae). Oecologia (Berlin) 78 (1989), 550-558.
STEVENSON, B. G. and D. E. DINDAL: Growth and development of *Aphodius* beetles (Scarabaeidae) in laboratory microcosms of cow dung. Coleopterist's Bulletin 39 (1985), 215-220.
SUDHAUS, W., REHFELD, K., SCHLUTER, D. and J. SCHWEIGER: Beziehungen zwischen Nematoden, Coleopteren und Dipteren in der Sukzession beim Abbau von Kuhfladen. Pedobiologia 31 (1988), 305-322.

VANCE, R. R.: The stable coexistence of two competitors for one resource. The American Naturalist **126** (1985), 72-86.
WASSMER, T. and P. SOWIG: Die coprophagen Kafer der Schafweide ,,Flachland" am Schonberg bei Freiburg. Veroffentlichungen fur Naturschutz und Landschaftspflege Baden-Wiirtemberg 1993 (in press).
YASUDA, H.: Reproductive properties of two sympatric dung beetles. *Aphodius haroldianus* and *A. elegans* (Coleoptera: Scarabaeidae). Res. Popul. Ecol. **29** (1987), 179-187.

Received: Februarys, 1993

Authors' adress: Dr. PETER SOWIG, Biologisches Institut I (Zoologie), AlbertstraBe 21 a, D-79104 Freiburg im Breisgau; Germany.
THOMAS WASSMER, Fakultat f. Biologic, Universitat Konstanz, Postfach 5560 M 618, D-78434 Konstanz, Germany.