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Selection of the spatial habitat of Coprophagous beetles in the Kaiserstuhl area near Freiburg (SW-Germany)

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Abstract

1. In an all-year-round survey of coprophagous beetles in a pasture in the Kaiserstuhl area (SW-Germany), cow-pats and sheep lumps were gathered from two field areas and one wooded area twice a month. 40,298 beetles belonging to 40 species of Scarabaeoidea and 14 of Hydrophilidae were detected. The small site on the Kaiserstuhl has the highest species diversity of Scarabaeoidea species among all local dung beetle coenoses described in Europe thus far.

2. In all seasons of the year, population density and biomass of dung beetles were higher on the open pastures than in the wooded pasture. Only in summer and on the coldest days of winter, values of both macrohabitats were approximately the same, which might be due to the mediated climate of wooded habitats in those seasons.

3. 11 out of 29 abundant species showed a clear preference for open macrohabitats, while only four prefered the wooded macrohabitat. All other species were eurytopic. Faunistic similarity was low among all three macrohabitats and did not show closer relationships between the two open pastures than between both of them and the wooded pasture.

4. Sheep lumps were more densely populated than cow-pats, whereas the latter contained a higher biomass in dung beetles. The cow-pat community was higher in species number as well as in diversity. Faunistic similarity between both dung beetle communities was minimal.

5. 13 out of 32 abundant dung beetle species preferred each dung type. Mean size of Scarabaeoidea dung beetles preferring sheep lumps was significantly lower than of those prefering cow-pats. Regardless their size difference, all but one Hydrophilidae species showed a pronounced preference for cow-pats.

6. Selection of the spatial habitats played a minor role in compartimentation of the total niche space of the dung beetle community as compared to temporal niche dimensions such as seasonality. As in the case of seasonality, *Aphodius* was best separated within the genus.

Keywords: Dung beetles, Scarabaeidae, Hydrophilidae. Geotrupidae, landscape type, forest, open pasture, dung type, cow-pats, sheep lumps.

Resume

1. Au cours d'une etude d'un an sur les coleopteres coprophages d'un paturage dans la region de Kaiserstuhl (sud-ouest de rAllemagne), des bouses de vaches et des crottes de moutons ont ete ramassees dans deux champs et un bois deux fois par mois. On a recense 40.298 coleopteres appartenant a 40 especes de Scarabaeoidea et 14 d'Hydrophilidae. Le petit site de Kaiserstuhl offre

la plus grande diversite specifique de Scarabaeoidea de toutes les biocenoses locales de bousiers decrites en Europe a ce jour.

2. A toutes les saisons, la densite de population et la biomasse des bousiers sont plus elevees dans les champs que dans le bois. En ete et pendant les jours les plus froids de 1'hiver seulement, les valeurs sont approximativement les memes pour les deux macro-habitats, ce qui peut etre du au climat modere des habitats boises pendant ces periodes.

3. 11 sur 29 especes abondantes presentent une preference nette pour les macrohabitats ouverts, et quatre preferent le macrohabitat boise. Toutes les autres especes sont eurytopiques. La similarite faunistique est faible entre les trois macrohabitats et ne presente pas de relation plus etroite entre les deux paturages ouverts qu'entre ces deux derniers et le paturage boise.

4. Les crottes de moutons sont plus densement peuplees que les bouses de vaches, mais ces dernieres contiennent une biomasse de bousiers plus elevee. La communaute des bouses de vaches est plus importante en nombre d'especes ainsi qu'en diversite. La similarite faunistique entre les deux communautes de bousiers est minimale.

5. 13 sur 32 especes de bousiers abondantes ont une preference pour chaque type de dejection. La taille moyenne des Scarabaeoidea preferant les crottes de moutons est significativement plus petite que celle des bousiers preferant les bouses de vaches. Quelles que soient leurs differences de taille, toutes les especes d'Hydrophilidae sauf une ont une preference marquee pour les bouses de vaches.

6. La selection de 1'habitat spatial joue un role mineur dans la compartimentation de 1'espace total de la niche des communautes de bousiers par comparaison avec les dimensions temporelles de la niche telles que les saisons. Comme dans le cas des saisons, *Aphodius* est la mieux separee dans le genre.

INTRODUCTION

CAUSE'S competitive principle (GAUSE, 1934) and HUTCHINSON'S question: "Why are there so many kinds of animals?" (HUTCHINSON, 1959) are milestones on the controversely led discussion on the presence or absence of competition between species. Empirical studies can provide data on this question for testing hypotheses of population and theoretical biology and may furtheron be essential for nature conservation and management (WASSMER, 1995). The total living space of an animal can be subdivided into temporal dimensions such as seasonality and succession, and spatial dimensions such as macro-/ microhabitats. There are plenty of studies on seasonality in dung beetles (e.g. HANSKI, 1980; HOLTER, 1982; DE GREEF & DESIERE, 1984; LUMARET & KIRK, 1987; AVILA & PASCUAL, 1988; WASSMER & SOWIG, 1994), fewer on succession (e.g. MOHR, 1943; VALIELA, 1969; HANSKI & KOSKELA, 1977), macrohabitat (LANDIN, 1961; RAINIO, 1966; HANSKI & KOSKELA, 1977) and microhabitat (LANDIN, 1961; RAINIO, 1966; HANSKI & KUUSELA, 1983; SOWIG & WASSMER, 1994) most of them lacking wintertime information. In the first part of a one year survey, I described the phenology of dung beetles in the Kaiserstuhl area including wintertime (WASSMER, 1994). This second part describes the differentiations within the dung beetle community according to two important dimensions of the macro- and microhabitat selection, the type of landscape and the type of dung all during the year.

METHODS

The location of the investigation, the Schelinger Weide (pasture), belongs to the central Kaiserstuhl (48°07 N; 7°41 E, approx. 400 m). Its position in the Upper Rhine Valley and on the lee side of the

Vosges (foehn), provides a favourable climate which is very mild by central European standards: yearly mean temperature 9.9°C, short and mild winters (mean temperature in January: 1.0°C) and a low total yearly precipitation of 664.9 mm. The actual climate and the biogeographic history during the postglacial warm period (Atlanticum) provided for a richness of mediterranean and pontic elements in the flora and fauna of the Kaiserstuhl. The Schelinger Weide is the only pasture left in the Kaiserstuhl area, which today is a famous wine growing region. It consists of two valleys covering a total area of approx. 520,000 m^2. A maximum of 30 head of small breed cattle originating from different extensive pastures all over Europe (predominantly *Aberdeenus angus)* and a flock of 30 sheep have grazed on the pasture all year round for over 15 years. History of stock farming on the Schelinger Weide is at least 90 years old. Enclosure of the cattle is not possible because of short water supply; cattle and sheep move freely all over the pasture area. For more details on the location refer to WASSMER *et al.* (1994).

For the purpose of this investigation, three sampling areas with great differences among their habitat structures were selected at the northern end of one of the two valleys:

- Area 1: Unshaded open field, exposition SSW-S, inclination 10°, deep soil (>30 cm) above loess and minimal erosion due to treading, vegetation cover 85-90%.
- Area 2: Unshaded open field, exposition SE-ESE, inclination 30°, shallow soil (< 10 cm) above Essexites (volcanic rock) with strong erosion due to treading. Vegetation covers 40-60% of the ground.
- Area 3: A wooded part of the pasture with only a small inclination (<5°) on deep soil.

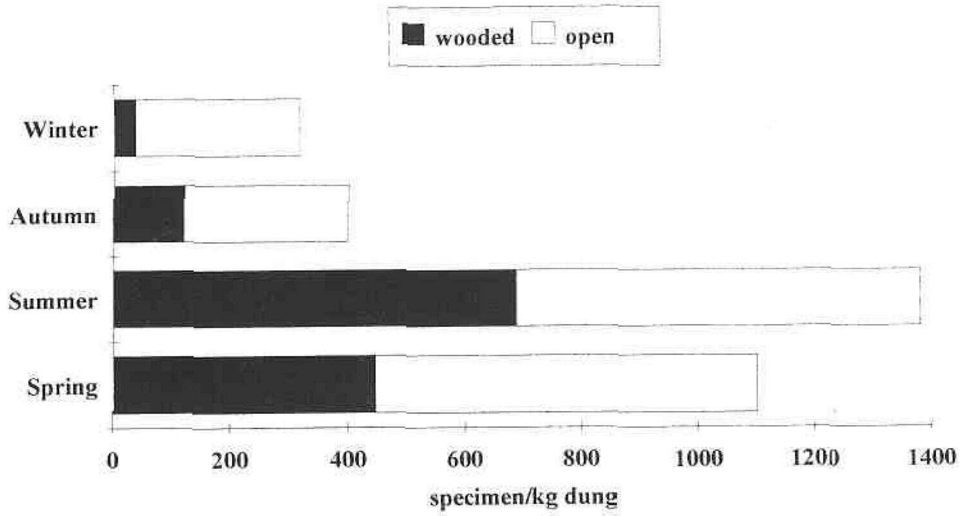
From April 14, 1992 until March 31, 1993, cow-pats (total 501.8 kg) and sheep lumps (total 62.9 kg) from each of the three sampling areas were collected and weighed separately (area 1: 185.4 kg; area 2: 182.7 kg and area 3: 196.7 kg, respectively; all weights in kg fresh weight) around the 1st and again around the 15th of every month. Beetles which were located directly beneath the dung pats were also collected, but no soil samples were taken. Due to this fact results may be biased with a systematic error in the case of paracoprid beetles. In order to minimize the influence of differing dung age, all available age classes were sampled in approximately equal quantities. Beetles were extracted by flotation (MOORE, 1954). Identification of species was carried out using the field guides of KRELL & FERY (1992) and MACHATSCHKE (1969) for the Scarabaeoidea, and of VOGT (1971) for the Hydrophilidae, mainly on living specimens, which were provided with dung and taken back to the pasture the next day. Only specimens from difficult species were preserved using Scheerpeltz solution (65% Ethanol, 5% Acetic Acid und 30% Aqua dest.) and identified with the help of a set of stereo lenses. It was not possible to perform a quantitative distinction among the closely related pairs of species: *Onthophagus taurus* Schreb. & *O. illyricus* Scop, (in my study *O. taurus* sensu lato); *O. ovatus L. & O. joannae* Goljan (= *O. ovatus* s.l.) and *O. fracticornis* Preyssl. & *O. similis* Scriba (= *O. fracticornis* s.l.), since the time consuming preparation of genitalia could only be carried out as a spot check in order to save most of the animals which were easily distinguishable from less related species. Klaus-Ulrich GEIS (Freiburg) and Frank-Thorsten KRELL (Wlirzburg) helped me to verify the presence of all six species. Biomass of species was estimated by using beetle dry weights obtained according to HANSKI & KOSKELA (1977), LUMARET & KIRK (1987) and WASSMER (1991).

RESULTS

Macrohabitat (landscape type: woodland vs. open field; Appendix A)

In all seasons of the year, except in summer and the coldest days of the year (December, 15th, 29th and January, 13th), population density was higher in the open pasture areas than in the wooded area (fig. 1).

Diversity and evenness were greatest in the open field 2, followed by the other open habitat (sampling area 1) and were lowest in the wooded area (fig. 2).



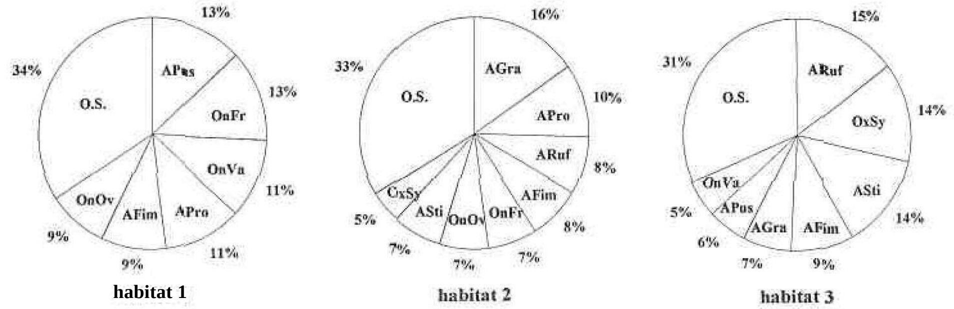


FIG. 2. - Dominance structures of the three macrohabitats (sampling areas). The open habitat 1 is determined by six main species (according to ENGELMANN, 1978) which accounted for about 2/3 of the species community (BRILLOUIN-Index 2.82, evenness 0.75). Dominance structure of open macrohabitat 2 was determined by ten main species. Eight species were necessary to make up 2/3 of the species community (SC) which is reflected by the highest diversity among the three sampling areas (BRILLOUIN-Index 2.89, evenness 0.79). Dominance structure of the wooded macrohabitat 3 was determined by nine main species. Seven species represented 2/3 of the SC. BRiLLOUiN-Index was 2.75 - evenness 0.74. Abbreviations: ADis: *Aphodius distinctus;* AFim: *Aph. fimetarius;* AGra: *Aph. granarius;* APay: *Aph. paykulli',* APro: *Aph. prodromus* APus: *Aph. pusillus;* ARuf: *Aph. rufus;* ASti: *Aph. sticticus.* OnFr: *Onthophagus fracticomis;* OnOv: *Ont. ovatus;* OnVa: *Ont. vacca.* OxSy: *Oxyomus sylvestris.* O.S.: other species.

TABLE I. - *Preferences of dung beetles for shaded or unshaded macrohabitats (percent of total occurrence of specimen per kilogram dung). Explanations: particular silvicole species occur almost exclusively in the wooded area (< 10% in open pastures); silvicole species occur less than 25% in open pasture areas; eurytopic species occur approx. 25-75% on either open or wooded pastures; pratinicole species occur less than 25% in the wooded area; particular pratinicole species occur almost exclusively in open pasture areas (< 10% in the wooded area).*

particular silvicole species:
none

silvicole species:
Oxyomus sylvestris; Aphodius rufus', Geotrupes spiniger; [A. sticticus (26% in open areas)].

eurytopic species:
Onthophagus vacca, O. coenobita; Aphodius distinctus, A. paykulli, A. fimetarius, A. rufipes, A. granarius, A. pusillus; Sphaeridium bipustulatum, S. scarabaeoides, S. lunatum; Cercyon haemorrhoidalis, C. pygmaeus, C. quisquilius.

pratinicole species:
Copris lunaris; Onthophagus verticicornis, O. ovatus, O. fracticornis; Aphodius arenarius, A. foetens, A. prodromus, Cryptopleurum minutum.

particular pratinicole species:
Aphodius sphacelatus, A. biguttatus, [Onthophagus taurus (13% in the wooded area)].

Fifteen species prefered macrohabitat 1. Within these species there were five of all six *Onthophagus* species (the distribution of *Ont. coenobita* did not show any difference from an equal distribution), all three *Sphaeridium-species, Aphodius biguttatus, A. fimetarius, A. prodromus, A. sphacelatus* and *A. pusillus* as well as *Cercyon pygmaeus* and *Cryptopleurum minutum.* The open pasture area 1 has a warmer exposition (SSW) and deeper soil than area 2.

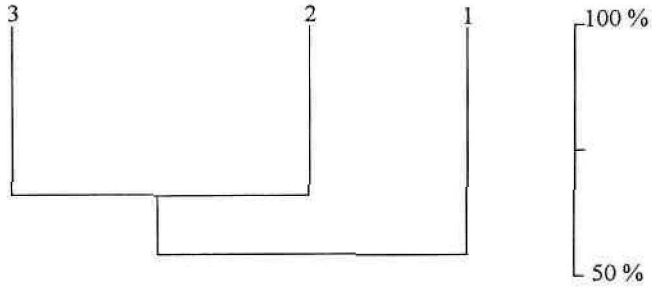
Only three species could be found significantly more frequently in macrohabitat 2 than in any of the two other sites: *Aphodius arenarius, A. granarius* and *A. foetens* (all statistics χ^2, $p<0.05$, normalized to the same amount of dung in all classes). The first and last of these species were described as psammophilous (KOCH, 1989a). Due to strong erosion on the thin soil crust, the Essexites were exposed and desintegrated into sandy soil. Diversity and evenness of open pasture 2 were highest among the three macrohabitats due to the dominance structure being evenly distributed among 10 main species (fig. 2).

Analysis of the faunistic similarity between macrohabitats, indexed by the RENKONEN-matrix, showed the higher values for areas 2 and 3 (67%). There was no clear separation of communities between the open fields and the wooded area (fig. 3).

When defining three resource classes which correspond to the sampling areas and a minimum niche overlap (PIELOU, 1970) of the species (weighted according to COLWELL & FUTUYMA, 1971) within one group at a rate of approx. 75%, four groups are clearly distinguishable (fig. 4):

1. *Geotrupes spiniger, Aphodius sticticus, A. rufus* and *A. rufipes,* as well as *Oxyomus sylvestris* and *Cercyon haemorrhoidalis.* All species had a strong preference for the wooded sampling area.

2. *Aphodius granarius* (maximum niche overlap of any other species 71.4%). More than 2/3 of the total occurrence of this species was on sampling area 2.



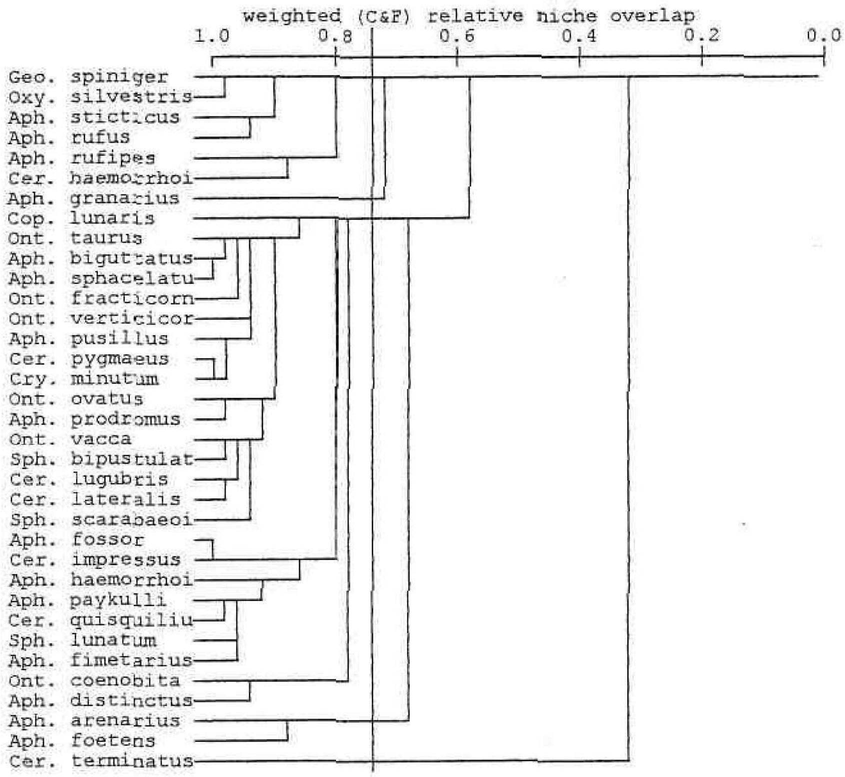


FIG. 4. - Cluster analysis (WPGMA) based on weighted (COLWELL & FUTUYMA, 1971) relative niche overlaps. Species filter: specimen numbers 20-3501; grouping according to niche dimension macrohabitat. The isolated position of *Cercyon terminatus* should be treated with caution, because this very small species is difficult to distinguish from *C. pygmaeus.*

3. *Copris lunaris', Onthophagus taurus, O. fracticornis, O. verticicornis, O. ovatus, O. vacca* and *O. coenobita; Aphodius biguttatus, A. sphacelatus, A. pusillus, A. prodromus, A. fossor, A. haemorrhoidalis, A. paykulli, A. fimetarius*

and *A. distinctus; Sphaeridium bipustulatum, S. scarabaeoides* and *S. lunatum; Cercyon pygmaeus, C. lugubris, C. lateralis, C. quisquilius* and *C. impressus,* as well as *Cryptopleurum minutum.* All species had a strong preference for the open pasture area 1.

4. *Aphodius arenarius* and *A. foetens* (maximum niche overlap of any other species 67.4%). As *Aphodius granarius* (Cluster 2), these two species showed a strong preference for area 2. In contrast to this species, *Aphodius arenarius* and *foetens* were more restricted to area 2 (psammophily) and were less frequent on the wooded area 3.

Comparing mean niche overlaps concerning the niche dimensions season (WASSMER, 1994) and microhabitat, much greater values could be found in the case of macrohabitat selection (total mean 0.79) which could be interpreted as macrohabitat playing a minor role in differentiation of the total niche (spatial and temporal) of species. Intrageneric niche overlaps of *Onthophagus, Sphaeridium* and *Cercyon* were significantly higher than between different genera which might indicate similar preferences on landscape type within one genus (table II). Within *Aphodius* (16 species) a small but significantly lower intrageneric mean niche overlap could be determined. This genus is greater in number of species than all other genera. The coexistence of various taxonomically and ecologically closely related species might be reflected by these findings.

TABLE II. - *Weighted (COLWELL & FUTUYMA, 1971) relative mean niche overlaps of species within and between genera. Statistics according to Mann-Whitney's U-test.*

Species filter: 20-3501 specimens — Biotop group: macrohabitat

Genus	Species number	Mean niche overlap: Within genus	Mean niche overlap: Between genera	Significance of the difference U-Test
Geo.	1	–	0.460	–
Cop.	1	–	0.753	–
Ont.	6	0.837	0.716	p< 0.001
Oxy.	1	–	0.443	–
Aph.	16	0.638	0.673	p<0.01
Sph.	3	0.894	0.767	p<0.05
Cer.	7	0.776	0.710	p<0.05
Cry.	1		0.734	–

Microhabitat (dung type; Appendix B)

According to the density of colonization, sheep lumps seemed to be a more attractive microhabitat as compared to cow-pats. Because larger species colonize the latter more frequently, biomass is higher in cow-pats (fig. 5). Values for diversity (BRiLLouiN-Index 3.00, evenness 0.77) and species number (49) were higher in the cow-pat community (sheep lumps: BRILLOUIN Index 2.57, evenness 0.72, species number 37).

It took nine species to result in 2/3 of the species community in cow-pats. There was not a pronounced ranking among the main species which resulted in a diverse and evenly distributed community (fig. 6). Already six species represented 2/3 of the sheep lump community.

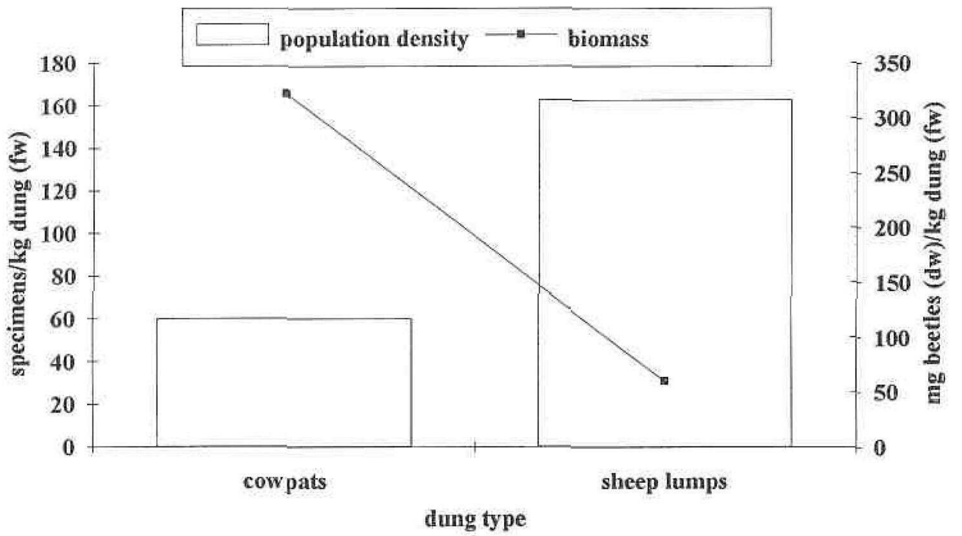


FIG. 5. - Population densities and biomasses of both dung types. Abbreviations: dw = dry weight; fw = fresh weight.

Gradations were well developed: *Aphodius prodromus*, the most frequent species, was almost twice as frequently present as the second *A. pusillus* (fig. 6). Faunistic similarity between both dung types, indexed by RENKONEN-matrix was 57.5% (according to the SoERENSEN-matrix: 86,1%).

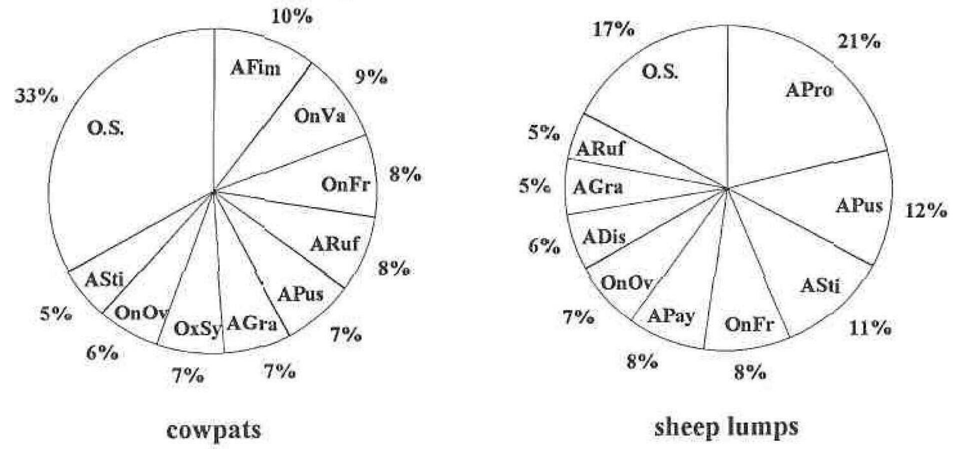


FIG. 6. - Dominance structures of the cow-pat and the sheep lump communities. The cow-pat community was determined by nine main species (according to ENGELMANN, 1978) which accounted for about 2/3 of the species community (SC). Dominance structure of the sheep lump community was also determined by nine main species, but only six species were necessary to make up 2/3 of the SC which was reflected by a lower diversity as compared to the cow-pat community. Same abbreviations as in Fig. 2.

Thirteen species significantly preferred either cow-pats or sheep lumps, respectively (x^2-test; $p<0.05$; standardized on the same amount of fresh dung in both classes).

• Within the Aphodiinae, cow-pats were preferred by: *Aphodius fossor* (0% in sheep lumps), *A. haemorrhoidalis* and *A. rufipes* (mean size 25.7 mg) while *A. arenarius, A. biguttatus, A. distinctus, A. granarius, A. paykulli, A. prodomus, A. pusillus, A. rufus, A. sphacelatus* and *A. sticticus* (mean size 3.1 mg) were found more frequently in sheep lumps. The pattern of distribution of *A. foetens* and *A. fimetarius* as well as *Oxyomus sylvestris* (mean size 7.3 mg) did not allow to reject the zero hypothesis of an even distribution. Selection of dung type based on body size was significant (p = 0.019, N = 15, two-tailed Kruskall-Wallis Anova). All of the other six *Aphodius* species were too rare to be tested.

• Of the Coprinae only *Onthophagus taurus s.l.* and *O. vacca* (mean size 36.8 mg) preferred cow-pats, whereas *O. fracticornis s.l., O. ovatus* and *O. verticicornis* (mean size 11.5 mg) were detected inhabiting sheep lumps more frequently than expected. *Copris lunaris* and *Onthophagus coenobita* were found in both of the substrates, as expected. Due to the small number of species (N = 6) within this group, selection of dung type based on body size was not significant (p = 0.180, two-tailed Kruskall-Wallis Anova). All of the other three tunnelers were too rare to be tested.

• Selection of dung type by body size in all more abundant Scarabaeoidea species together (N-23) was significant (p = 0.012, two-tailed Kruskall-Wallis Anova).

• Within the Hydrophilidae the large *Sphaeridium* species (mean size 7.8 mg) as well as most of the small *Cercyon* and *Cryptopleurum* species (7 of 14 species, mean size 0.7 mg) significantly preferred cow-pats *(S. bipustulatum* 1%, *C. lateralls* 0% in sheep lumps). With the exception of *Cercyon quisquilius* which was as frequent in both dung types, all of the other Cercyon species were too rare to allow a x^2test.

When defining two resource classes which correspond to the two dung types under investigation and a minimum niche overlap of the species within one group at a rate of approx. 70%, three groups were clearly distinguishable (fig. 7).

1. Cow dung species: *Geotrupes spiniger; Copris lunaris, Onthophagus taurus* and *O. vacca', Aphodius haemorrhoidalis, A. fossor, A. fimetarius, A. foetens* and *Oxyomus sylvestris; Sphaeridium bipustulatum, S. scarabaeoides, S. lunatum, Cercyon pygmaeus, C. lugubris, C. lateralis, C. quisquilius, C. haemorrhoidalis* and *Cryptopleurum minutum* (maximum niche overlap of any other species approx. 45%).

2. Generalists (slightly preferring sheep lumps): *Onthophagus verticicornis, 0. coenobita, O. ovatus* and *O. fracticornis', Aphodius rufus, A. granarius, A. arenarius, A. pusillus* and *A. sticticus* as well as *Cercyon impressus.*

3. Sheep dung species: *Aphodius biguttatus, A. sphacelatus, A. prodromus, A. paykulli* and *A. distinctus* (maximum niche overlap of any other species approx. 64%).

Comparing the mean niche overlaps concerning the niche dimensions season (WASSMER, 1994) and microhabitat, much greater values could be found in the case of the microhabitats selection, the same being the case for the macrohabitat. Within the genera *Sphaeridium, Onthophagus* and *Cercyon* mean niche overlaps

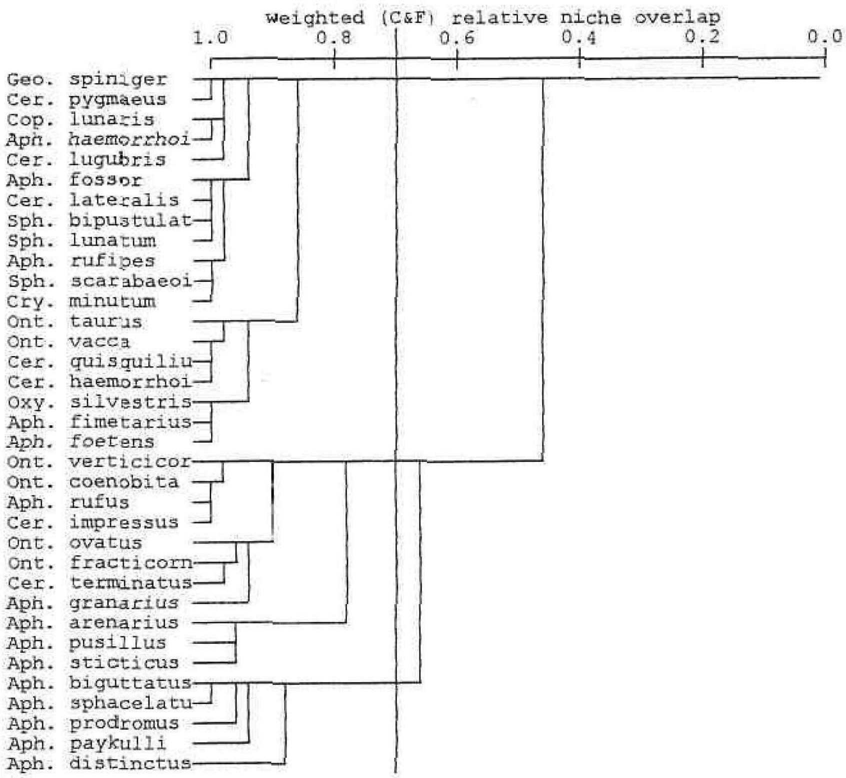


FIG. 7. - Cluster analysis (WPGMA) based on weighted (COLWELL & FUTUYMA, 1971) relative niche overlaps; Species filter: specimen numbers 20-3501; grouping according to the niche dimension microhabitat.

were significantly higher than the intergeneric values, reaching within *Sphaerldium* values of nearly 100% (table III). Within *Aphodius* (16 species) niche overlaps were least. In contrast to the other multispecific genera, intrageneric mean niche overlap was not significantly higher than between genera.

DISCUSSION

Macrohabitat

Some of the species in the Kaiserstuhl area could be found much more frequently in the wooded area than in the open pastures, but none of these species could be assigned to a particular silvicole species (table I). CAMBEFORT & HANSKI (1991) characterized 6 out of 32 northern temperate and 5 out of 39 southern temperate Scarabaeoidea, respectively, as species that prefer forestal habitats, but did not assign any of these to be an exclusive specialist. In the same way, LUMARET & KIRK (1987) found species with a distinct preference for wooded areas, but none of these species completely avoided open habitats.

Although it is believed that central Europe was covered by forests on at least 90% of its area before the development of agriculture, this does not mean that these natural undisturbed forests (climax formations) were in a large area, dense and dark. Modern mosaic or gap theories on climax forests (e.g. SHUGART, 1984; PICKETT & WHITE, 1985; MULLER-DOMBOIS, 1987 and REMMERT, 1991) prove them to be patchy over a greater geographical scale, showing a mosaic of patches of different vegetation covers and developmental stages interrupted by natural clearings. In consequence, climax forests offer a broad pallete of different spatial habitats, showing great differences in abiotic and biotic factors as illumination, water balance, availability of food and presence of predators and competitors. Due to the low abundance and variety of big dung producing forest animals, one can assume that there were only a few exclusive specialists on forest habitats among dung beetles (e.g. *Aphodius zenkeri)*, preferring clearings rather than dense and dark: climax forests. These silvicole species are the real indigenous species in central Europe after the Atlanticum (postglacial warm periode). In contrast, particular pratinicole species may have been adventitious species, immigrating into central Europe from southern and eastern grasslands since the development of agriculture with its clearings and stock-farming.

In the vicinity of Montpellier (France), *Onthophagus coenobita* preferred illuminated oak forests (LUMARET & KIRK, 1987), whereas this species seems to be a generalist in the Kaiserstuhl area. As in my results, HANSKI & KOSKELA (1977) detected a clear preference by *Aphodius rufipes* and *A. rufus* for wooded areas in southern Finland, whereas RAINIO (1966) supports this result only in the case of *A. rufipes.*

In his book on the ecology of central European beetles, KOCH (1989a) calls all coprophagous Hydrophilidae which could be found on the Kaiserstuhl eurytopic or ubiquist. I can support this with the exception of *Cryptopleurum minutum* (>75% of its occurrence was on open pasture areas). Within the Scarabaeoidea, the same author describes *Onthophagus verticicornis* as being particular silvicole and *Geotrupes spiniger* as particular pratinicole species (KocH, 1989*b*). In contrast to this, I found *O. verticicornis* to be a pratinicole and *G. spiniger* to be a silvicole species.

LANDIN (1961) confirmed *Aphodius sticticus* and *A. paykulli* to be silvicole species in Sweden, although they may also be found in exposed areas. In contrast to my investigation, he could not determine either *Oxyomus sylvestris* nor *Aphodius rufus* to be more frequent in wooded areas.

Differences among the findings of investigations from different geographic latitudes reflect the variability within widely distributed species which are an ultimate reason for their expansion. In hot and dry regions a sensitive species has to settle on more shady macrohabitats, whereas the same species can settle in open and exposed areas in cold temperate climates. Table IV illustrates the most important climatic factors differing between open and wooded areas. In spring, autumn and most of the winter, open habitats provide a more favourable microclimate for most of the dung beetles than wooded habitats. On the other hand, wooded areas become more attractive in summer and on the coldest winter days, because the tree tops provide a mediated microclimate (fig. 1).

TABLE IV. - *Microclimatic differences between wooded and open habitats (according to WILMANNS, 1984, supplemented).*

to the mediterranean fauna element, favouring warm and mild habitats. In the Kaiserstuhl area, only *O. coenobita*, which is believed to be a palaearctic species, did not favour the open habitats. Contrasting with *Onthophagus*, the paracoprid species of the holarctic genus *Geotrupes*, favoured the wooded area, where soil profile was even deeper than in area 1.

Area 2 had an extremely shallow soil and was located on a steep incline (30°) above the bottom of the valley. On a high percentage of the total area of this sampling site, volcanic rock (Essexite) was exposed. Although only a few species showed any preference for this sampling site, it showed the highest values in diversity and evenness (fig. 2). This puzzling result might be due to the even distribution of most of the species of the dung beetle community, without pronounced dominance of any species.

Cluster analysis on the relatedness of the species communities of the three sampling sites, based on the RENKONEN indices, demonstrated no clear separation between woodland species and open field species, but showed a high degree of independence among all three sites (fig. 3).

Microhabitat

The most prominant difference between cow-pats and sheep lumps is the tenfold size of the first. Differences in physicochemical contents are less obvious, as both dung producers belong to ruminant Bovidae. Other than size, microclimatic behaviour might be the most important factor for habitat selection among dung beetles (table V).

RAINIO (1966) found approximately twice as many dung beetles in sheep lumps as compared to the same weight of cow-pats. My results yielded a relation of 3:1. In contrast to this, biomass in cow-pats was more than six times higher than in sheep lumps, because most of the large and medium sized dung beetle species showed a pronounced preference for the larger microhabitat. If there is a choice between large cow-pats and small sheep lumps, a large dung beetle, having higher demands on space and nutrition, should waste no time by visiting the smaller microhabitat but select the larger cow-pats. Because this strategy is valid for both sexes, it increases the probability of mating. In contrast to this, selection of small dung pats is a good strategy for a small dung beetle, which is seeking cover, nutrition or a mate, because it can avoid competition with the larger beetles.

Although oviposition sites especially of dung dwelling species (endocoprids) are often very different from feeding and mating sites (e.g. older in succession, lower content in water and nutrients - BREYMEYER, 1974; OTRONEN & HANSKI, 1983), both criteria are also valid for the selection of oviposition sites, because larvae of larger beetles have higher demands of space and nutrition than the smaller larvae of small species, and they are superior competitors, often killing larvae of other species as well as of conspecifics (MADLE, 1934).

LUMARET *et al.* (1992) described changes in community structure after shifting grazing from sheep to cattle in a mediterranean pasture biotope. Diversity decreased while total number of beetles, biomass and species number increased. In contrast to this result, diversity was higher in the cow-pat community on the Kaiserstuhl, which might be due to the simultaneous presence of both dung types for a long period of time. Beside this difference, LUMARET *et al.* (1992) used cow dung to trap beetles on both sites, which might have led to a different attraction of beetles. In their study, the proportion of rollers and small tunnelers within the cow dung community decreased after the shifting of grazing, whereas the proportion of medium sized and large tunnelers and dwellers increased. In my study, among the Scarabaeoidea, larger dung beetle species prefered cow-pats, while smaller ones prefered sheep lumps. In contrast to this, all but one small Hydrophilidae species of the genus *Cercyon* as well as *Cryptopleurum minutum* prefered cow-pats in the same way the medium sized *Sphaeridium* species did. As members of the primary water living Hydrophilidae, these species seem to be extremely sensitive to desiccation and extreme temperatures (SOWIG & WASSMER, 1994). As a consequence of the smaller size of sheep droppings and the fact that there is no development of a mediating crust, sheep lumps could be dangerous and insecure microhabitats for Hydrophilidae dung beetles, as microclimatic measurements have shown (LANDIN, 1961; WASSMER, 1991). As in HANSKI & KUUSELA (1983) *Cercyon quisquilius* was the only Hydrophilidae species to be abundant in sheep dung, although this species did not appear as a sheep dung specialist but as a microhabitat generalist.

TABLE V. — *The most important differences between the two dung types under investigation, which might determine the microhabitat selection of a dung beetle.*

a) KAHNERT *et al.* (1990); b) OLECHOWICZ (1974); c) MADLE (1934); d) LANDIN (1961)

Concerning the dung type, both communities are well separated with a similarity of only approximately 58% (RENKONEN-Index), which is mainly due to different dominance structures (SoERENSEN-Index 86%). As in HANSKI & KUUSELA (1983) the sheep dung community was dominated by a few species (fig. 6), whereas the cow-pat community showed a rich and evenly distributed community with nine main species (fig. 6). Cluster analysis confirms specialists in both dung types, as well as a generalist group (fig. 7). Within all multispecific genera, intrageneric niche overlaps were higher than between different genera. Difference was not significant in *Aphodius,* which might indicate a higher level of segregation within this genus as compared to *Onthophagus, Cercyon* or *Sphaeridium* (table III).

The results on paracoprid beetles may be biased especially in the case of sheep droppings, because no soil samples beneath the pads were taken. Nevertheless one could expect the influence of this systematic error of methodology being minimal because small and medium sized species of the genus *Onthophagus* were found more frequently within and below sheep lumps, than in cow-pats.

The pasture near Schelingen in the Kaiserstuhl area is a dry and lean area. As a consequence of the poor water supply, only sheep and small modest cattle can exploit the pasture all year round. This fact might have amplified the selection pressure on optimal foraging concerning dung type and landscape type, which is known not to be very rigid in intensive pastures.

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APPENDIX A. - *Occurrence (abundance) of 51 species of Scarabaeoidea and Hydrophilidae on the three macrohabitats. Macrohabitats 1 and 2 are open fields, whereas macrohabitat 3 is a wooded pan of the pasture (for more details see Methods). Nomenclature and systematics according to KRELL & FERY (1992) and VOCT (1971).*

APPENDIX B. - *Occurrence (abundance) of 51 species of Scarabaeoidea and Hydrophilidae on two types. Nomenclature and systematlcs according to KRELL & FERY (1992) and VOGT (1971).*

dung type	cow-pats	sheep lumps	total
fresh weight of dung [kg]	501.832	62.912	564.744
Aphodius arenarius Ol.	126	59	185
Aphodius biguttatus Germ.	65	137	202
Aphodius contaminatus Hbst.	2	0	2
Aphodius distinctus Mull.	84	566	650
Aphodius fimetarius L.	3101	400	3501
Aphodius foetens F.	59	8	67
Aphodius fossor L.	76	0	76
Aphodius granarius L.	2029	561	2590
Aphodius haemorrhoidalis L.	1151	67	1218
Aphodius luridus F.	5	2	7
Aphodius paykulli Bed.	633	788	1421
Aphodius prodromus Brahm	1257	2186	3443
Aphodius pusillus Hbst.	2165	1197	3362
Aphodius rufipes L.	441	7	448
Aphodius rufus Moll	2285	491	2776
Aphodius scrutator Hbst.	4	0	4
Aphodius sphacelatus Panz.	93	226	319
Aphodius sticticus Panz.	1540	1111	2651
Aphodius subterraneus L.	1	0	1
Aphodius zenkeri Germ.	3	0	3
Aphodius maculatus Sturm	1	0	1
Cercyon haemorrhoidalis F.	916	89	1005
Cercyon impressus Sturm	18	4	22
Cercyon laminatus Sharp.	1	0	1
Cercyon lateralis Marsh.	36	0	36
Cercyon lugubris Ol.	32	1	33
Cercyon melanocephalus L.	11	1	12
Cercyon pygmaeus 111.	511	22	533
Cercyon quisquilius L.	154	17	171
Cercyon terminatus Marsh.	19	6	25
Cercyon unipunctatus L.	2	1	3
Copris lunaris L.	75	4	79
Cryptopleurum minutum F.	615	7	622
Euoniticellus fulvus Gze.	2	0	2
Geotrupes spiniger Marsh.	22	1	23
Geotrupes stercorarius L.	2	0	2
Maladera holosericea Scop.	2	0	2
Onthophagus coenobita Hbst.	62	13	75
Onthophagus fracticornis Preyssl. s.l.	2494	869	3363
Onthophagus ovatus L. s.l.	1875	731	2606
Onthophagus taurus Schreb. s.l.	513	43	556
Onthophagus vacca L.	2694	281	2975
Onthophagus verticicornis Laich.	357	65	422
Oxyomus sylvestris Scop.	1972	260	2232
Rhyssemus germanus L.	2	0	2
Sphaeridium bipustulatum F.	557	1	558
Sphaeridium lunatum F.	1247	.6	1253
Sphaeridium scarabaeoides F.	739	12	751