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# Seasonality of coprophagous beetles in the Kaiserstuhl area near Freiburg (SW-Germany) including the winter months

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**Abstract**

In an all-year-round survey of coprophagous beetles in a pasture in the Kaiserstuhl area (SW-Germany), dung pats were gathered twice a month (on the 1st and the 15th). 40,298 beetles belonging to 38 species of Scarabaeoidea and 14 of Hydrophilidac, were detected. The small site on the Kaiserstuhl has the highest species diversity in Scarabaeoidea species of all local dung beetle coenoses described in Europe so far.

A comparison of monthly dominance structures of the species community between the Kaiserstuhl and warm temperate pastures in the south of Spain yields similarities on both the subgenus and species levels.

Analyses of the phenological distributions of 34 abundant dung beetle species show a high degree of specialisation among all taxonomic and phenologic groups, most prominently among the ***Aphodius.*** There are even species which occur predominantly during the winter months, which might be due to low interspecific competition in these months and favourable synchronisation of mating and reproduction. Cluster analysis confirms eight phenological groups and proves the very structuring nature of the niche dimension season.

Beside the qualitative separation of species, there was remarkable segregation in the biomass of species in the different months. "Dwellers" (endocoprid species) of the subfamily Aphodiinae showed the most pronounced separation, followed by small "Tunnelers" (paracoprid species) belonging to the ***Onthophagus*** big "Tunnelers" of the ***Copris*** and ***Geotrupes*** and small Hydrophilidae "Dwellers" of the genus ***Cercyon. Sphaeridium*** did not show phenological separation among its three species.

**Keywords:** Dung beetles, Scarabaeidae, Hydrophilidae, Geotrupidae, phenology, winter, hibernation, seasonal segregation.

**Resume**

Dans une etude s'etendant sur un an et portant sur le scarabee coprophage d'un paturage a Kaiserstuhl (sud-ouest de l'Allemagne) nous avons rassembl6 des amas d'excrement tous les 1[ers] et 15 de chaque mois. Nous avons recense 40.298 scarabees appartenant a 38 especes de Scarabaeoidea et 14 d'Hydrophilidae. Le petit site de Kaiserstuhl compte la plus grande diversity d'especes de Scarabaeoidea de toutes les communautes de bousiers connues en Europe. Une comparaison des structures mensuelles de dominance de communaute d'especes entre Kaiserstuhl et les pfiturages temper6s chauds du sud de l'Espagne font apparattre des similitudes au niveau des sous-genres et des especes.

Les analyses des distributions phenologiques de 34 especes abondantes de bousiers montrent un degre eleve de specialisation parmi tous les groupes taxonomiques et phenologiques, le principal £tant ***Aphodius.*** On retrouve meme des especes qui apparaissent principalement pendant les mois d'hiver, ce qui pourrait etre du a une competition interspecifique faible durant ces mois et a une bonne synchronisation entre les accouplements et la reproduction. Une analyse en amas confirme l'existence de huit groupes et prouve la nature tres structurante du modele saisonnier d'exploitation.

En plus de la separation qualitative des especes, on observe une remarquable segregation des especes dans la biomasse au cours des differents mois. Les membres de la sous-famille Aphodiinae montrent la separation la plus nette, suivie par les petits tunneliers ***Onthophagus,*** les grands tunneliers ***Copris*** et ***Geotrupes*** ainsi que les petits Hydrophilidae du genre ***Cercyon.*** II n'existe pas de separation phenologique chez les trois especes de ***Sphaeridium.***

## INTRODUCTION

A great number of papers describe local dung beetle coenoses at temperate latitudes, predominantly in Northern Europe (e.g. LANDIN, 1961; RAINIO, 1966; HANSKI & KOSKELA, 1977) and Central Europe (e.g. HANSKI, 1980; GEIS, 1981; HOLTER, 1982; DE GRAEF & DESIERE, 1984; WASSMER & SOWIG, 1994), but also in Southern Europe (e.g. LUMARET & KIRK, 1987; AVILA & PASCUAL, 1988a), Eastern Europe (e.g. BREYMEYER, 1974; OLECHOWICZ, 1974; ADAM, 1986), Asia (YASUDA, 1984) and North America (e.g. MOHR, 1943; VALIELA, 1969). In the majority of the investigations, phenology proved to be one of the most important factors in structuring dung beetle biocoenoses. Therefore the lack of a phenological study, which covers the winter months of the cold temperate latitudes, is most astonishing. It reflects the old assumption that there is no insect life during the cold season. Recent research on the physiological abilities of Scarabaeidae and beetles in general prove them to be extremely resistant against cold temperatures (ZACHARIASSEN, 1980; STOREY *et al,* 1993). This paper provides data for a pasture biotope in the south of Germany during the whole year.

## METHODS

The location of the investigation, the Schelinger Weide (pasture) belongs to the central Kaiserstuhl (48°07N; 7°41E, 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 small total yearly precipitation of 664.9 mm. The actual climate and the biogeographic history during the postglacial warm period (Atlanticum) provided a richness of mediterranean and pontic elements in the flora and fauna of the Kaiserstuhl. The Schelinger Weide is the only pasture which was left in the whole of the Kaiserstuhl, since the area is nowadays a famous wine growing region. It consists of two valleys with 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 graze in the pasture all year round for over 15 years. Enclosureing of cattle is not possible because of bad water supply; cattle and sheep move freely all over the pasture area. For more details on the location refer to WARMER ***et al.*** (1994).

Sampling was carried out on two open and one wooded pasture area. From April 14, 1992 till March 31, 1993, cow pats (sum: 501.8 kg; minimum-maximum: 2470-18355 g; mean: 7068 g; standard deviation (SD): 2906 g; median: 6435 g) and sheep lumps (sum: 62.9 kg; minimum-maximum: 72-2195 g; mean: 898.7 g; SD: 446.6 g; median: 860 g) from each of the 3 sample areas were collected and weighed separately (area 1: 185.4 kg; area 2: 182.7 kg and area 3: 196.7 kg respectively) 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. 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). Determination of species was carried out with the help 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 between the closely related pair of species: ***Onthophagus taurus*** Schreb. & ***O. illyricus*** Scop, (in my study ***O. taurus*** sensu lato); ***O. ovatus*** L. & ***O. joannae*** Goljan ***(=0. ovatus*** s.l.) and ***O. fracticornis*** Preyssl. & ***O. similis*** Scriba (= ***O. fracticornis*** s.l.), because 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 easy to distinguish from less related species. Klaus-Ulrich GEIS (Freiburg) and Frank-Thorsten KRELL (Tubingen) helped me in verifying the presence of all 6 species. Biomass of species was estimated by using beetle dry weights obtained according to HANSKI & KOSKELA (1977), LUMARET & KIRK (1987) and WASSMER (1991).

## RESULTS

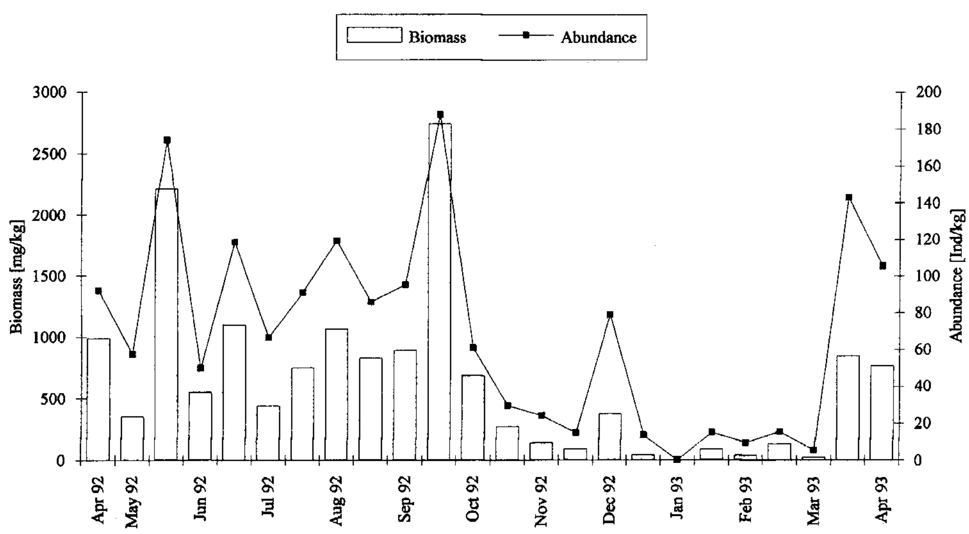
### Faunistic diversity

The dung beetle population in the Kaiserstuhl area is highly varied in species. During a single year I was able to detect no fewer than 38 species of Scarabaeoidea and 14 of Hydrophilidae (see Appendix). In comparison with other methodologically similar studies from all over Europe, the Kaiserstuhl site shows the highest number of species in Europe (LANDIN, 1961; BREYMEYER, 1974; HANSKI & KOSKELA, 1977; HANSKI, 1980; HOLTER, 1982; DE GRAEF & DESIERE, 1984; Ricou & LOISEAU, 1984; LUMARET & KIRK, 1987; WASSMER & SOWIG, 1994). 60% of all *Aphodius* species in Denmark could be detected in the Kaiserstuhl area within one year and in a small sample area. In Denmark only 6 *Onthophagus* species, most of them extremely rare, belong to the national fauna (HOLTER, pers. comm.), whereas in this study 9 species could be found in quite high numbers. The species community in the Kaiserstuhl area is even more diverse than in all described mediterranean pastures. In a recent review, LUMARET & KIRK (1991) presented data on 9 pastures in the Languedoc (SW-France). The highest species number was 27 species of Geotrupidae and Scarabaeidae; the corresponding relation for the pasture near Schelingen is 38 species.

The variety of species is due to both, the local climate which enables mediterranean, pontic and Central European species to live there, and to the biogeographical position of the Kaiserstuhl in the middle of the western corridor (Burgundian gate), through which species could resettle in Central Europe after the last glacial epoch (WASSMER *et al*, 1994).

## Seasonality of total abundance, biomass, species numbers and diversity of dung beetles

During the year, there was a considerable fluctuation of both abundance and biomass of dung beetles (fig. 1). Abundance and biomass developed more or less proportional, there are two big maxima on May 19, 1992 and on September 16, 1992, which reflect maximum numbers of spring- and autumn generations of bivoltine species and still high numbers of univoltine spring- or summer species respectively. The third largest maximum in number on March 15, 1993 mainly consists of *Aphodius prodomus* Brahm. Most Aphodiinae are relatively small, therefore the increase in total numbers relative to the first March sample is much greater than that of the biomass. From mid October until the beginning of March, numbers and biomass levels were below the average for each half month. Only on December 1, mild weather interrupted this "winter rest" (Germ. Winterruhe). There was no clear "summer rest" (Germ. Sommerruhe) as are found in warm temperate pasture ecosystems during the summer drought (AVILA & PASCUAL, 1988a; LUMARET & KIRK, 1987). During the period between April and October, species numbers and diversities were above the average for each month (fig. 2).




FIG, 1. - Total abundances (adult beetles per kg dung fresh weight) and biomass (mg beetles as dry weight per kg dung fresh weight) of coprophagous beetles for every half month sample throughout the year.

## Dominance structures of the months and similarities between seasons

Figure 3 shows relative dominance structures of the species community (SC) for all months of the year (1st and 15th sample combined). Dominance classes were used according to ENGELMANN (1978). Core or main species could be eudominant (>32%), dominant (10.0-31.9%) or subdominant (3.2-9.9%).

• January 1993: SC was dominated by *Aphodius paykulli* Bedel (97.3 %). In addition there were only 3 more species, most abundantly *Aphodius distinctus*

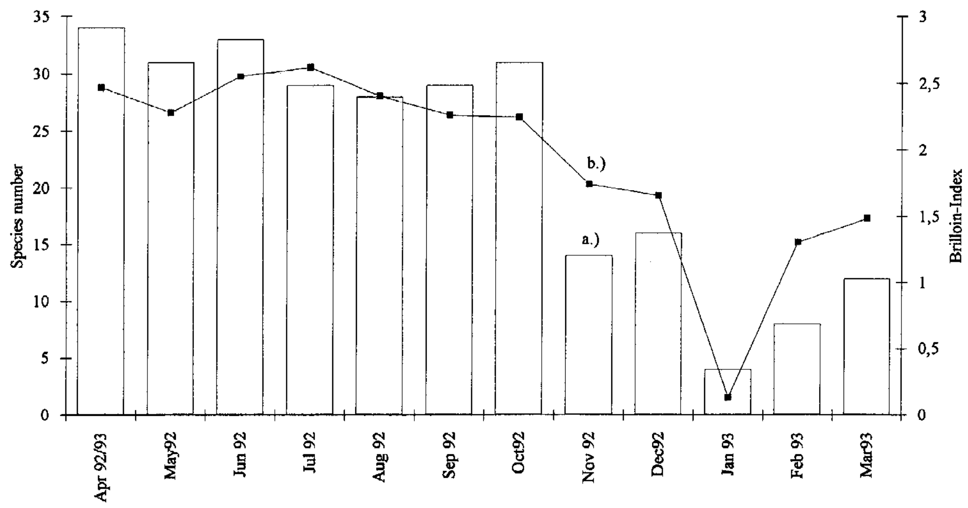



FIG. 2. - Species numbers a.) and diversities (Brillouin-Index) b.) for every month of the year. The application of biocoenological software made it necessary to connect 2 sample days.

Miiller (1.5%) which also belongs to the subgenus *Chilothorax* Motsch. (Syn. *Volinus* Mulsant & Rey).

• February 1993: SC was dominated for 2/3 of the time by only 2 species: *Aphodius paykulli* (47.2 %) and *A. prodromus* (33 %). Next were *A. fimetarius* L. (8.8%) and *A. sphacelatus* Panz. (5.9%). Dominant subgenera were *Chilothorax* (50.6 %) and *Melinopterus* Mulsant *(A. prodromus & A. sphacelatus:* 38.9 %). *Onthophagus fracticornis* was the only Coprinae at 0.5%. As in January, there were no Hydrophilidae.

• March 1993: As in the preceding month, two species alone made up 2/3 of the SC. Subgenus *Melinopterus* clearly dominated; *Chilothorax* decreased to 8.7%. Seasonal ubiquists *{Aphodius fimetarius* and *Onthophagus fracticornis)* were at 24.7 % and indicate the change from winter to spring. *Oxyomus sylvestris* Stephens, an Aphodiinae which is not restricted to dung feeding, contributed 5 %.

• April 1992/93: Because the investigation began on April 14th 1992, the April sample also includes March 31, 1993. April showed an evenly differentiated SC with the highest species number of the year, but only third according to the Brillouin-Diversity. Five species made up 2/3 of the SC. Early spring species appeared but did not dominate. *Aphodius prodromus* continued to be the most abundant species (21.9%), five species followed at approx. 5%: A. *granarius* L. (a spring-early summer species), *Onthophagus ovatus* and *O. vacca* L., both with a wide range from spring-autumn and seasonal ubiquists, *A. fimetarius* and *O. fracticornis.* The first generations of bivoltine Coprinae reached their peak (34.7 %). Hydrophilidae reached approx. 5 %

• May 1992: Four species represented almost 2/3 of the SC. The spring-early summer species *Aphodius pusillus* Herbst became dominant (34.1 %). *O. vacca* increased its rate to 17 %. *Cercyon haemorrhoidalis* Fabr. was the first Hydrophilidae in the year to become a major species of this month at 8.0%.

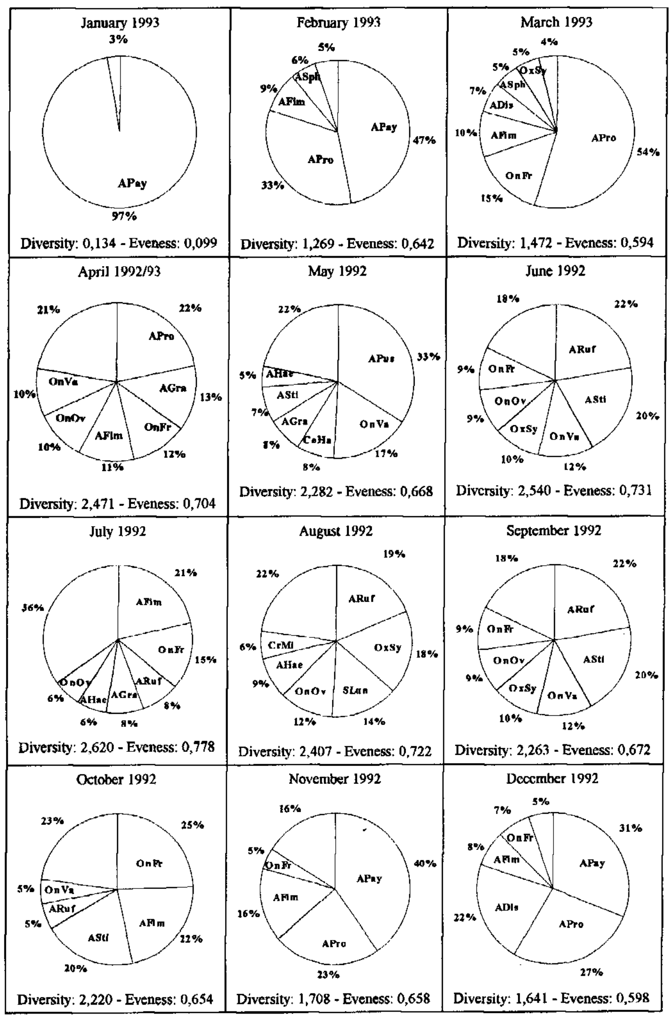



FIG. 3. - Dominance structures (relative numerical abundances) of the single months of the year. Abbreviations: ADis: ***Aphodius distinctus;*** AFim: ***Aph. fimetarius;*** AGra: ***Aph. granarius;*** AHae: ***Aph. haemorrhoidalis;*** APay: ***Aph. paykulli;*** APro: ***Aph. prodromus;*** APus: ***Aph. pusillus;*** ARuf: ***Aph. rufus;*** ASph: ***Aph. sphacelatus;*** ASti: ***Aph. sticticus.*** CeHa: ***Cercyon haemorrhoidalis.*** CrMi: ***Cryptopleurum minutum.*** OnFr: ***Onthophagus fracticornis;*** OnOv: ***Ont. ovatus;*** OnVa: ***Ont. vacca.*** OxSy: ***Oxyomus sylvestris.*** SLun: ***Sphaeridium lunatum.*** The blank sector stands for all other species. Diversity is measured as the Brillouin-Index.

In total Hydrophilidae reached 13.5%. *Aphodius sticticus* Panzer (7.3%) and *A. haemorrhoidalis* L. (4.6%) were two species of early summer-autumn.

• June 1992: Six species represented 2/3 of the SC. *Aphodius pusillus* was still the most abundant species at 21.0%. Second was *A. granarius* by 16.3 %. *O. vacca* reached the same relative abundance as in April (approx. 10%). Again *A. sticticus* was at 8%, while Hydrophilidae reached 16.3%.

• July 1992: In this month seven species made up 2/3 of the SC. Diversity and Evenness reached their annual maxima. The composition of the SC had changed completely, because spring and spring-autumn species were not present. The seasonal ubiquists *A. fimetarius* and *O. fracticornis* dominated this period of transition by 21.5% and 14.7% respectively. *A. granarius* (8.4%) was the only species of spring-summer to be a major species of the SC in this month. A newcomer to the group of main species was *A. rufus* Moll, by 8.4 %, a summer-autumn species, which indicated the change to midsummer. Hydrophilidae were at 20%.

• August 1992: Diversity decreased significantly: Four species constituted 2/3 of the SC. Brillouin-Index and Evenness fell below values for April. *A. rufus,* which first appeared in July, dominated this midsummer month (18.9%). *Oxyomus sylvestris,* which was last dominant in March, was second in numbers at 17.7%. For the first time since May a Hydrophilidae became a major species: *Sphaeridium lunatum* F. (14.4%) - in total Hydrophilidae reached their highest annual values (31.8%). Aphodiinae, which typically dominate cold temperate pastures, reached their annual minimum (51.6%; all months between June-August as well as October <60%).

• September 1992: Although five species were necessary to make up 2/3 of the SC, the Brillouin-Index proved this month to be less diverse than August. Again *Aphodius rufus* was the most abundant species (22.4 %) closely followed by *A. sticticus* (19.7%). *Onthophagus vacca* and *O. ovatus* signaled the beginning of autumn (10% each). Coprinae reached 34.0%.

• October 1992: SC was well represented with only three species (20% each): *O. fracticornis, A. fimetarius* and *A. sticticus.* Due to the dominance of the seasonal ubiquist *O. fracticornis* and remaining high values for the autumn generations of bivoltine species, Coprinae reached their maximum annual numbers (35.1 %).

• November 1992: Two species accounted for more than 60% of the SC: *Aphodius paykulli* which had been absent since February, became the most abundant species (40.4%), followed by *A. prodromus* (23.2%) and *A. fimetarius* (15.9%). Aphodiinae reached nearly 90% with predominant subgenera *Chilothorax* (43.6 %) and *Melinopterus* (25.9 %). Seasonal ubiquists were at 20.8 %. This species composition is typical for late autumn and early winter.

• December 1992: As in November, 2/3 of the SC were formed by 3 species. *A. paykulli* was only slightly more abundant than *A. prodromus:* 31.3 vs. 27.3%. Next came *A. distinctus* (21.9%). In total *Chilothorax* was at 53.4% and *Melinopterus* at 30.1%. All Aphodiinae reached 91.6%. *O. fracticornis* was the only Coprinae during the winter (7.0%).

Using a WPGMA (Weighted Pair Group Method using arithmetic Averages)-Cluster Analysis based on Renkonen's-coefficient, it is possible to define four biological periods when studying dung beetles (fig. 4): I. January is the only month of extreme midwinter; II. November and December and later from February until April were early winter and late winter periods. November and February were more closely related; III. May and June were early summer months and IV. July through to October were late summer periods.

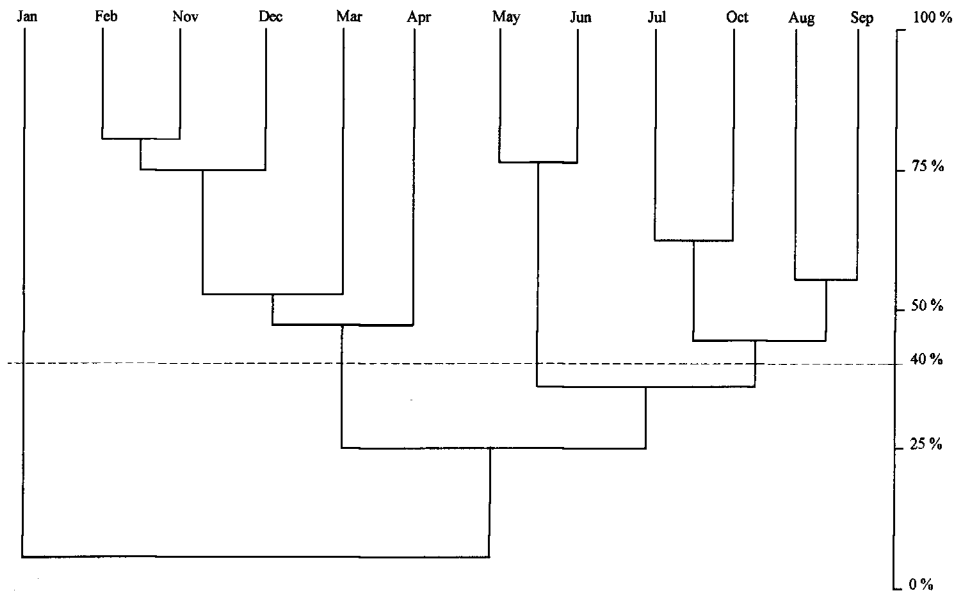



FIG. 4. - Taken a similarity in the monthly dominance structures of 40 %, four distinct clusters could be distinguished: I. November and December together with February till April; II. July till October (SC in July and October are more similar to each other than July compared with August or August compared with September); III. May and June; IV. January (similarity to any other month < 6 %).

## Utilization of the niche dimension season: phenological patterns and species groups

When defining 12 resource classes which correspond to the months of a year and a minimum niche overlap of the species within one group at a rate of 55 %, 8 groups are clearly distinguishable (fig. 5):

1. *Geotrupes spiniger, Onthophagus fracticornis* and *Aphodius fimetarius* (maximum niche overlap of any other species 42.1 %) (fig. 6).

2. *Onthophagus verticicornis* Laich; *Aphodius granarius, A. arenarius* Olivier and *A. biguttatus; Cercyon lugubris, C. impressus* Sturm and *C. quisquilius* (fig. 7).

3. *Aphodius sphacelatus* and *A, prodromus* (maximum overlap of any other species 47.4%) (fig. 8).

4. *Copris lunaris; Onthophagus taurus* and *O. ovatus; Aphodius haemorrhoidalis* and *Oxyomus sylvestris; Sphaeridium bipustulatum* F., *S. scarabaeoides* and *S. lunatum; Cercyon lateralis* Marsh, and *C. pygmaeus* 111., as well as *Cryptopleurum minutum* F. (fig. 9).

5. *Onthophagus vacca, O. coenobita* Herbst. and *Aphodius sticticus* (maximum overlap of any other species 48%) (fig. 10).

6. *Aphodius rufus, A. rufipes* and *A. foetens* F. (maximum overlap of any other species 48%) (fig. 11).

7. *Aphodius fossor* and *A. pusillus,* as well as *Cercyon haemorrhoidalis* (maximum overlap of any other species 22.6%) (fig. 12).

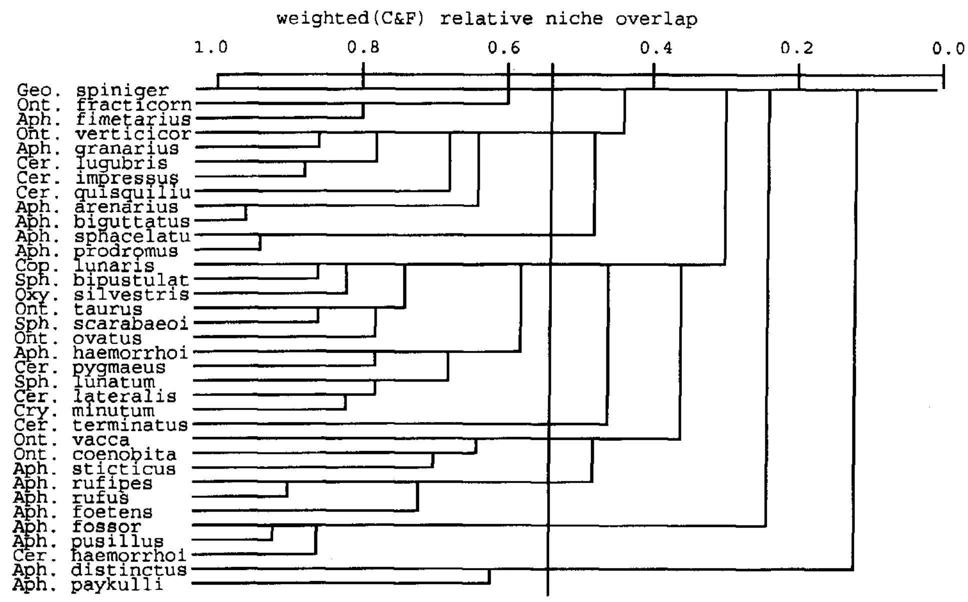



FIG. 5. - Cluster analysis (WPGMA) based on weighted (COLWELL & FUTUYMA, 1971) relative niche overlaps. Species filter: specimen numbers 20-3501; grouping after the niche dimension: month.

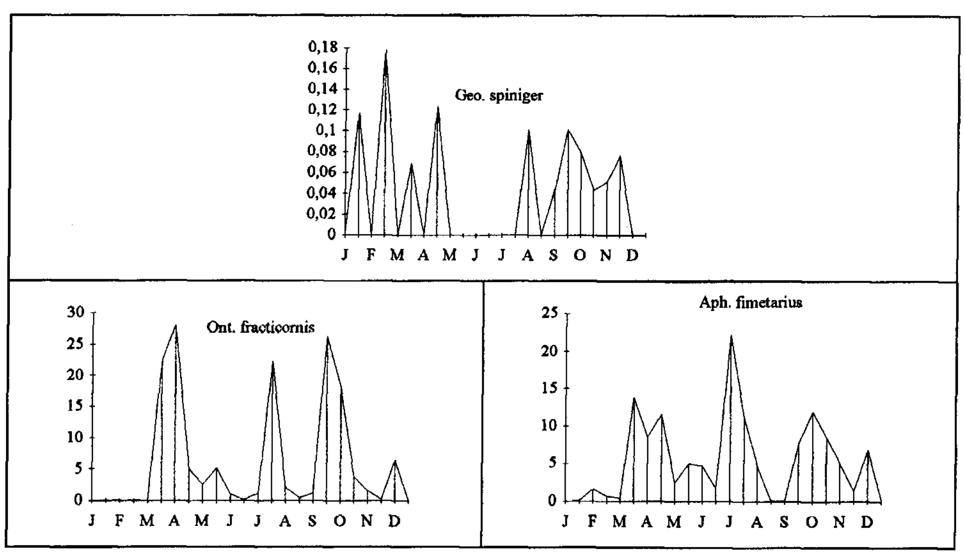



FIG. 6. - Cluster 1: Polymodal species that occur throughout the year. Abscissa: initials of the months (1st, 15th); ordinate: specimen per kg dung (fresh weight).

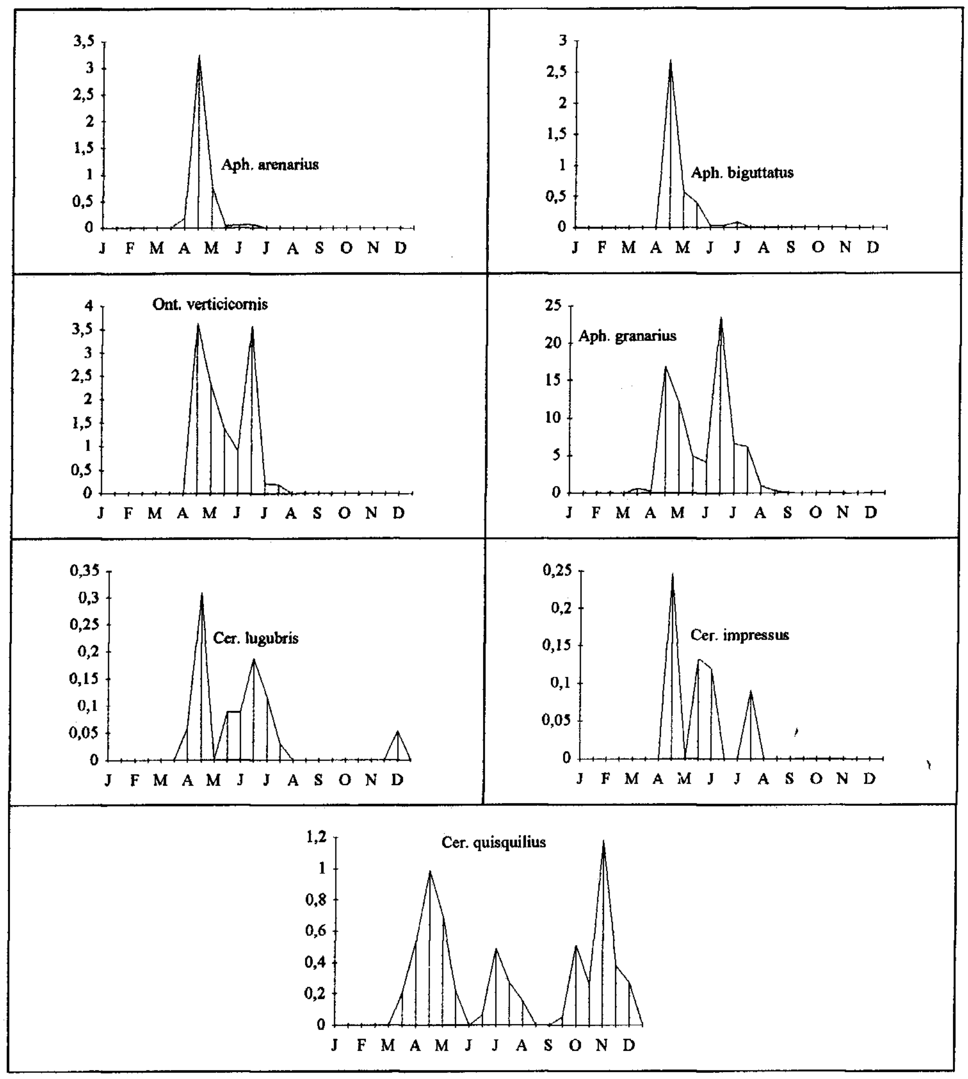



FIG. 7. - Cluster 2: Unimodal spring species and bi- or polymodal species that occur from spring till summer or autumn, with a pronounced peak in April. Axes as in Fig. 6.

8. *Aphodius distinctus* and *A. paykulli* (maximum overlap of all other species only 11.6%) (fig. 13).

In order to understand the position of the seasonal niche of a single species it is necessary to compare it with the phenology of the other species. For such a comparison, total biomass of a species is a better means than numerical occurrence would be, because it reflects species differences in terms of resource utilization. Most species grew in number between July 1 and October 1. This period

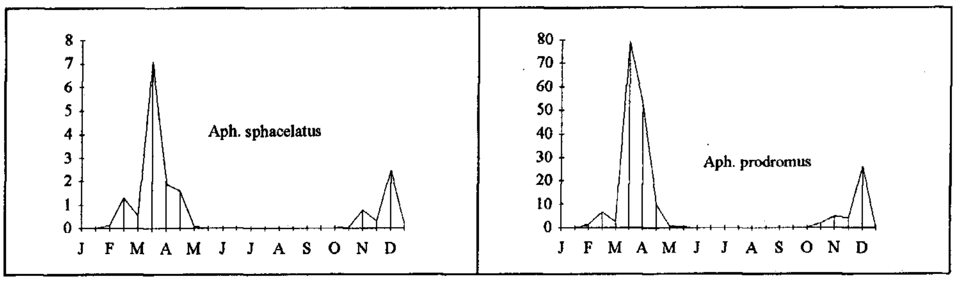



FIG. 8. - Cluster 3: Bimodal early spring and late autumn species. Axes as in Fig. 6.

corresponded to an intermediate minimum between the two maxima of bimodal *Onthophagus vacca,* the most dominant species of the whole sampling period. All the other spring and early summer species were much less abundant during times in which *O. vacca* is dominant. In general, the period between October 29 and March 2 (winter in a broad sense) is much less productive than any other period of the year. For further analyses it is more appropriate to follow the suggestion of DOUBE (1990) and to distinguish five species groups, because they show important differences in resource utilization due to body size and breeding type and following this, one can assume different competitive situations between and within these groups:

1. Large paracoprid Scarabaeidae and Geotrupidae (tunnelers >50 mg dry weight); only 2 species: *Copris lunaris* L. and *Geotrupes spiniger* Marsham were abundant enough to allow an evaluation of their distribution patterns. Beetles within this category dig faster and deeper than small paracoprids of the genus *Onthophagus,* therefore they avoid competition for breeding space underneath the dung pat. Due to their much larger size in relation to all other beetles in the SC, they consume much more dung for their nourishment and for the supply of their eggs. Because they dig faster than *Onthophagus,* they become superior competitors. They are more on the K-side of the r/K-continuum, showing low numbers of offspring, intensive brood care and reaching a lifespan over one year (ROMMEL, 1967; KLEMPERER, 1979, 1982) (fig. 14).

2. Small paracoprid Scarabaeidae (tunnelers <50mg dry weight): with the exception of two specimens of *Euoniticellus fulvus* Goeze, this group is exclusively represented by nine species of *Onthophagus,* ranging in size from 5.7 mg *(O. ovatus)* to 41.2 mg *(O. vacca).* Five of them were abundant enough to be included in data evaluation (fig. 15).

3. Dung dwelling (endocoprid) Scarabaeidae: 22 species of the genus *Aphodius* and *Oxyomus sylvestris,* ranging in size from 0.6 mg (A. *biguttatus* Germar) to 40.8 mg *(A. scrutator* Herbst). Seasonal distribution of the 10 most abundant species of *Aphodius* and *Oxyomus sylvestris* could be evaluated (fig. 16).

4. Large Hydrophilidae (>5 mg): genus *Sphaeridium* (3 species) (fig. 17).

5. Small Hydrophilidae (<5 mg) of the genus *Cercyon* (8 species) and 1 species of *Cryptopleurum* (fig. 18).

There are seasonal differences among all taxonomic and functional groups; nevertheless the degree of segregation varies greatly. Because there were only two large tunnelers, occurring in large numbers, figure 14 might be disappointing at a

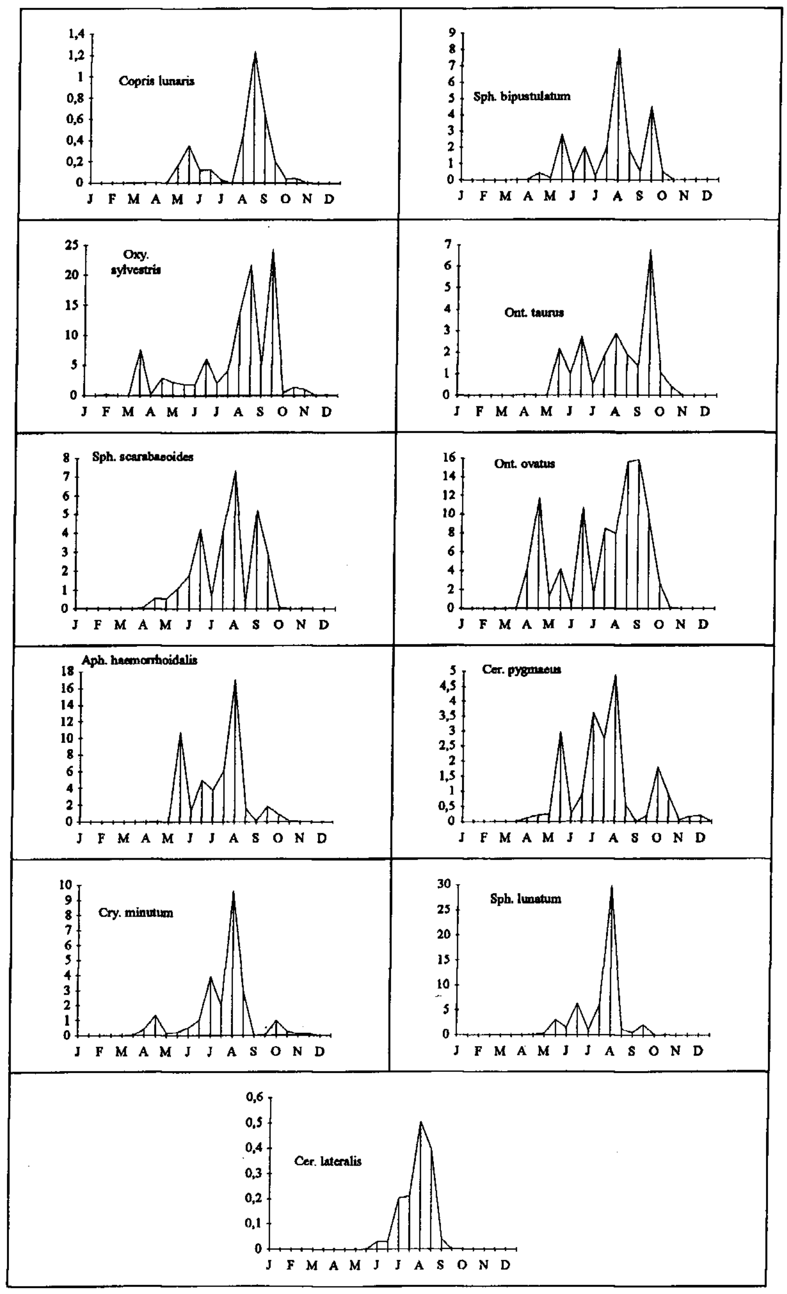



FIG. 9. - Cluster 4: Uni-, bi- or polymodal species of early-late summer or early summer till early autumn species, with their maximal abundance in August and September. Axes as in Fig. 6.

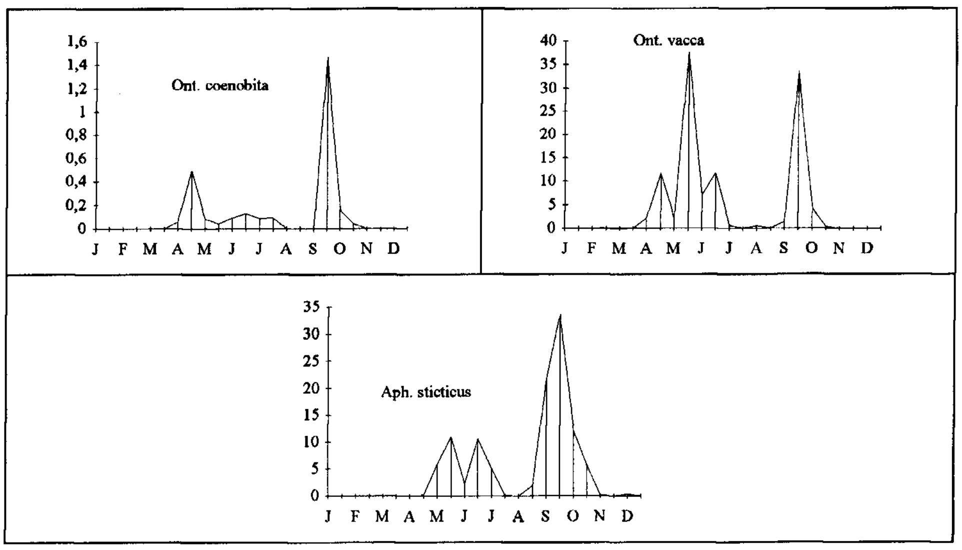



FIG. 10. - Cluster 5: Bimodal spring till autumn species with a first peak in April or May, disappearing in July or August with another peak in September. Axes as in Fig. 6.

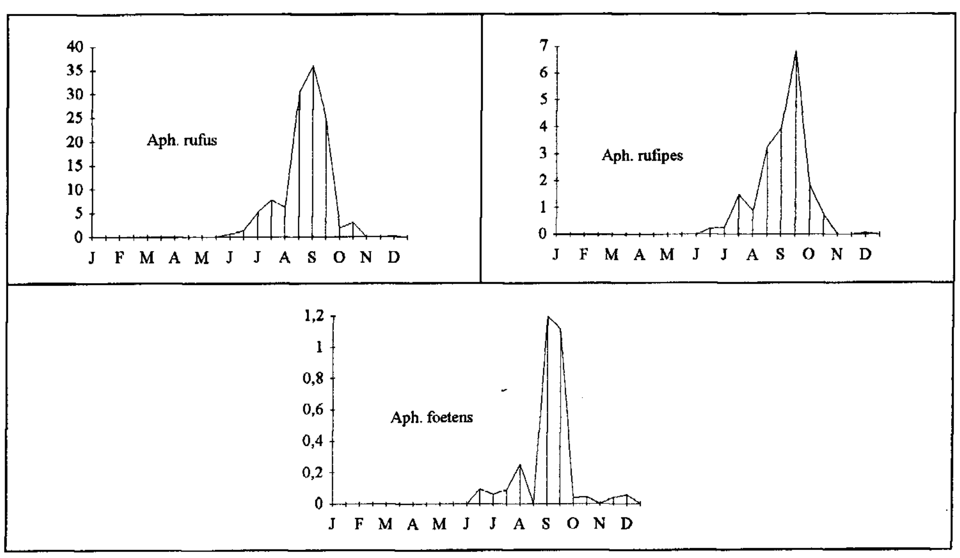



FIG. 11. - Cluster 6: Unimodal late summer till autumn species. Axes as in Fig. 6.

first glance. Nevertheless there is a clear distinction: *Copris lunaris* is dominant in summer, between the beginning of May and the beginning of September. From mid September until mid October, *C. lunaris* and *Geotrupes spiniger* occupy approximately the same proportion of biomass. Finally, in late autumn, winter and spring *Geotrupes spiniger* clearly dominates.

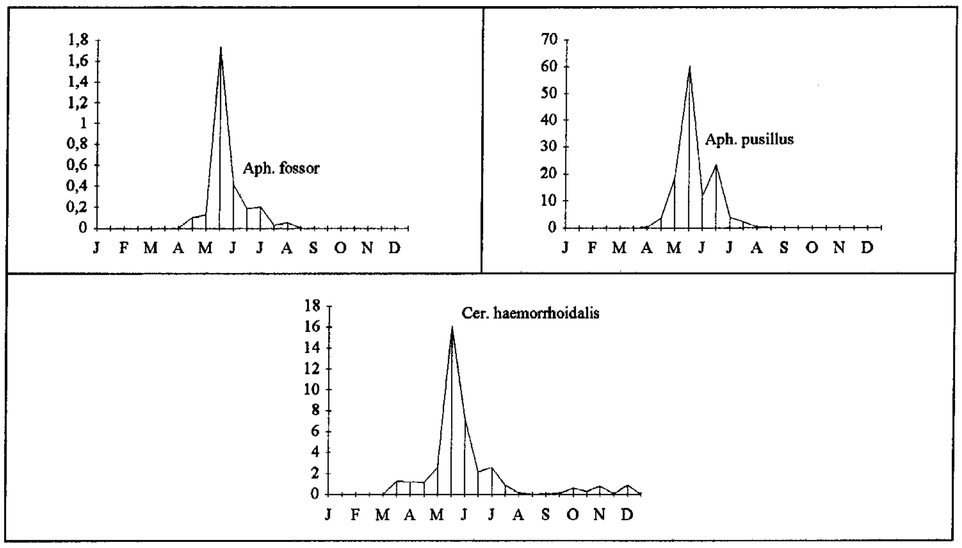



FIG. 12. - Cluster 7: Unimodal late spring till early summer species. Axes as in Fig. 6.

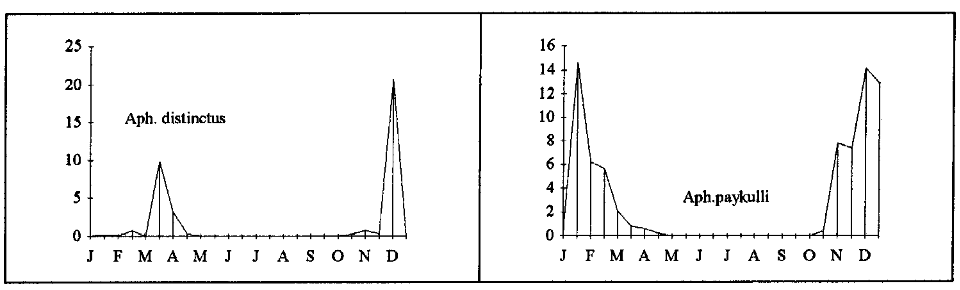



FIG. 13. - Cluster 8: Bimodal late autumn and early spring species and late autumn till early spring (winter) species. Axes as in Fig. 6.

As mentioned above, the 10 most abundant *Aphodius-species* show a far more noticeable segregation, including the winter months (rig. 16). There are spring species, spring-summer species, spring-autumn species, summer and autumn species and late autumn/winter-spring species. Within all seasonal groups there are additional sub segregations most prominent within the spring species.

Second in seasonal segregation are small tunnelers of the genus *Onthophagus* (fig. 15) and third, small hydrophilid dwellers of *Cercyon* and *Cryptopleurum* (fig. 18). For both groups the winter months are not used by any specialist. Lowest in seasonal niching are the three *Sphaeridium-species:* maxima and minima of all of these are more or less simultaneously present (fig. 17).

These findings are well represented by comparing mean niche overlaps (PIELOU, 1972) within and between genera. *Aphodius* (16 species) showed a significant lower mean overlap within the genus, than between species of other genera. In contrast,

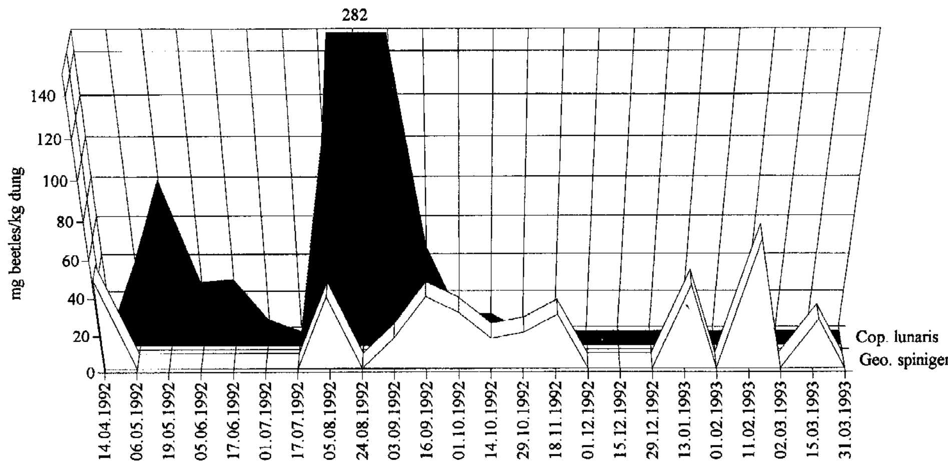
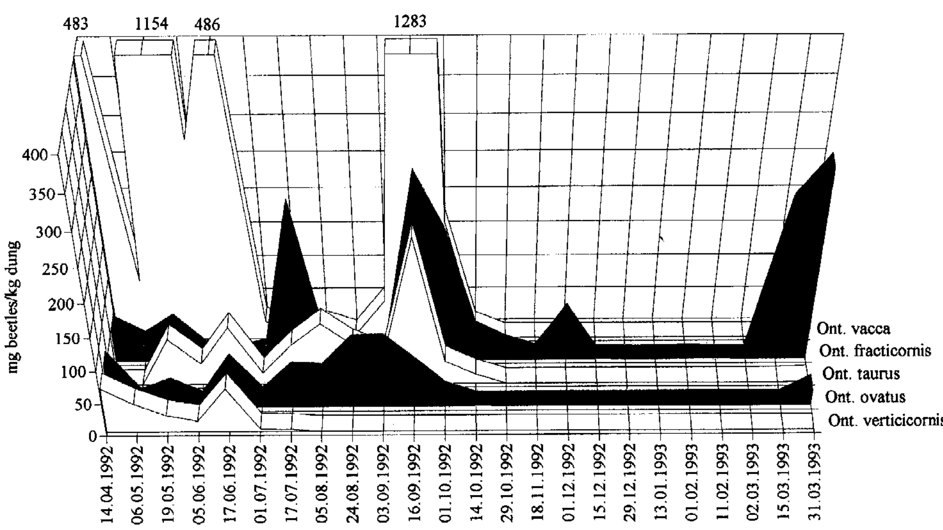



FIG. 14. - Seasonal segregation of large paracoprid Scarabaeidae and Geotrupidae. Abscissa: sampling date; ordinate: biomass.




*Onthophagus* (6 species) and more pronounced *Sphaeridium* (3 species), showed significantly higher mean overlaps within the genera. *Cercyon* (7 species) did not show a significant difference (table I).

## DISCUSSION

1. Seasonality of total occurrence (abundance), biomass, species numbers and diversity of dung beetles.

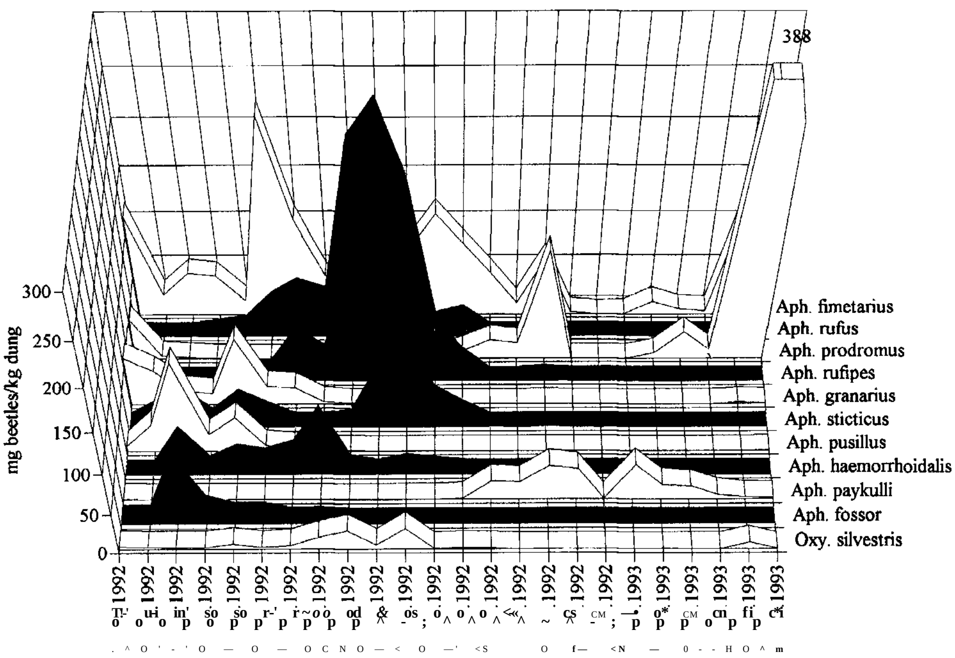



FIG. 16. - Seasonal segregation of dung dwelling Scarabaeidae. Axes as in Fig. 14.

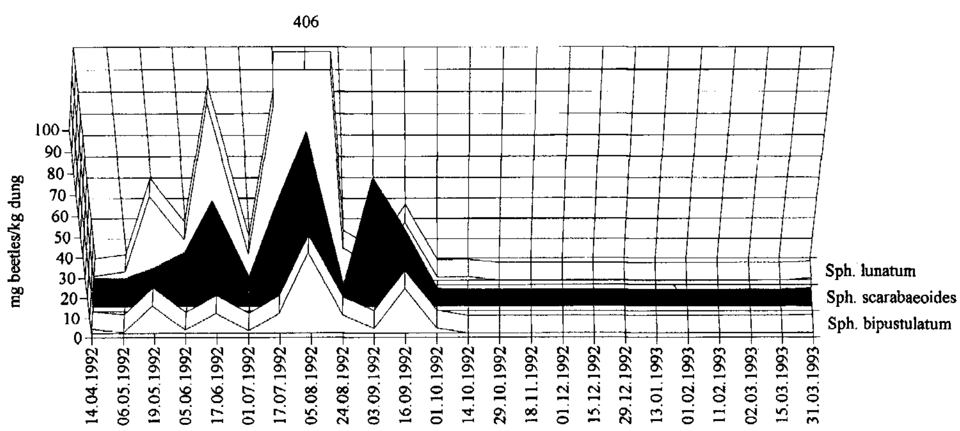



FIG. 17. - Seasonal segregation of large Hydrophilidae. Axes as in Fig. 14.

2. Dominance structures of the months and similarities between seasons.

3. Utilization of the niche dimension season: phenological patterns and species groups.

So far all phenological studies on dung beetles in cold temperate areas of Europe took place only between April and October and did not include the winter

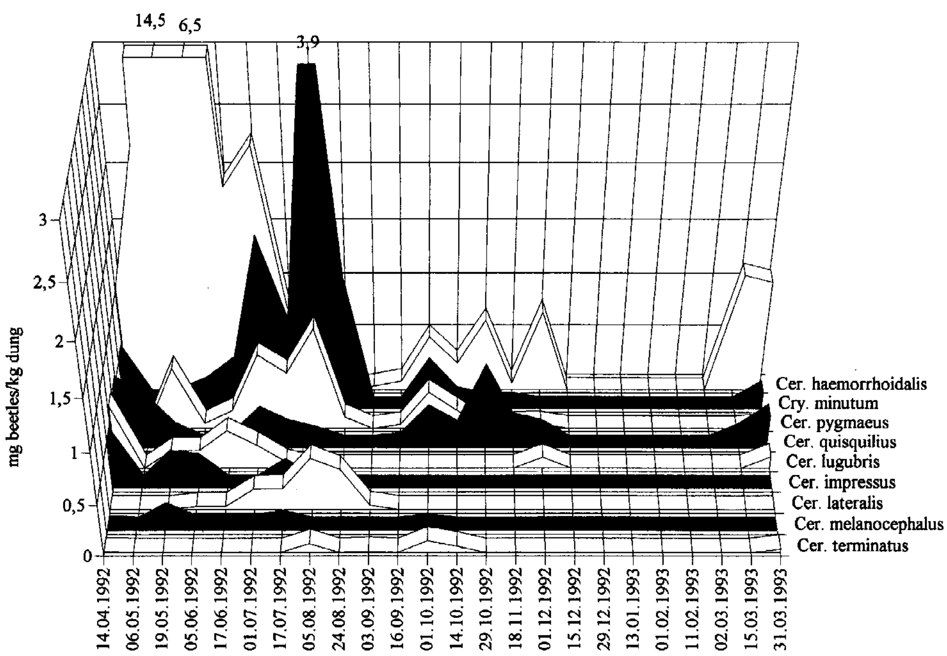



FIG. 18. - Seasonal segregation of small endocoprid Hydrophilidae. Axes as in Fig. 14.

TABLE I. - *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: month

| genus | species number | mean overlap within genus | mean overlap between genera | significance of the difference following U-Test |
|---|---|---|---|---|
| Geo. | 1 | – | 0.360 | – |
| Cop. | 1 | - | 0.382 | - |
| Ont. | 6 | 0.558 | 0.401 | p< 0.001 |
| Oxy. | 1 | - | 0.424 | - |
| Aph. | 16 | 0.261 | 0.319 | p< 0.001 |
| Sph. | 3 | 0.708 | 0.395 | p< 0.001 |
| Cer. | 7 | 0.377 | 0.350 | n.s. |
| Cry. | 1 | - | 0.363 | - |

months, therefore they can only partially be compared with this study. Some warm temperate pasture biotops were investigated throughout the year and allow a better comparison (LUMARET & KIRK, 1987; AVILA & PASCUAL, 1988a). In the Schelinger Pasture, phenologic emergence of adult beetles common in Northern, Central and Southern Europe, starts 1-2 months later than in the Sierra Nevada (Southern Spain - AVILA & PASCUAL, 1988a) but 1-2 months earlier than in Southern England (HANSKI, 1980), Denmark (HOLTER, 1982) or Belgium (DE GRAEF & DESIERE, 1984) and corresponds well with a gradient in latitude. Most species in the Kaiserstuhl area show a prolonged phenology as compared with the northern sites. As a result of the more favourable climate in early spring and late autumn, the yearly lapse of total beetle numbers and biomass per month is nearly the same at the Kaiserstuhl as compared with Spain (AVILA & FERNANDEZ-SIGLER, 1988; AVILA & PASCUAL, 1988a), but begins earlier and ends later in the year. In the Camargue, LUMARET & KIRK (1987) found a slow increase of species numbers between January and April, with a broad peak from May until July and a slow decrease until November. As at the Kaiserstuhl, December is richer in species than November, January and February. In the French Garrigue, species numbers and biomass show an intermediate minimum in July and August which corresponds to the summer drought period in the warm temperate climate (LUMARET & KIRK, 1987). There is a slight decrease in species numbers and biomass at the Kaiserstuhl during the summer, although the local climate does not have a real summer drought.

Much more noticeable are similarities between the dominance structures of the Schelinger Pasture and the Sierra Nevada (AVILA & PASCUAL, 1988*b*). Here the same or closely related species can be found, which are main species of the SC in the Sierra Nevada, one-three months before they become dominant at the Kaiserstuhl. Other pairs of species are phenologically similar but taxonomically less related (table II). Although the Sierra Nevada lies nearly twice as far south of the Kaiserstuhl than the Languedoc, similarities on the species level between the Kaiserstuhl and the Garrigue in Languedoc are much less noticeable. This might be due to the fact that pastures in the Garrigue and at the Kaiserstuhl are mainly hilly (<400 m), whereas pastures at the Sierra Nevada are montainous, subalpine or even alpine (700-2600 m). In the Languedoc, winter is the only season when Aphodiinae reach more than 10% of the total specimens (LUMARET & KIRK, 1987). Dominating species were *A. constans* (95,2%) and *O. coenobita* (2,9%). Phenologically and taxonomically similar or identical pairs of species between the Garrigue and the Kaiserstuhl are *O. joannae* vs. *O. ovatus s.l.* (which includes both species *sensu stricto),* and at both sites *A. haemorrhoidalis,* the only Aphodiinae at the Languedoc, which is frequent in summer in cow pats.

TABLE II. — ***Phenologically similar species pairs from the Kaiserstuhl and Sierra Nevada*** *(AVILA & PASQUAL, **1988b). The first 3 species pairs are taxonomically not very closely related, but inhabit the same temporal niche in either location (the last analogy is between two subgenera, which are not closely related). The forth and sixth species pair is made up of the same species in both locations (except*** Aphodius fimetarius, ***there is also*** A. foetidus ***within the same seasonal niche at the Sierra Nevada), whereas within the fifth species pair*** Onthophagus fracticornis ***s.l. is a collective species and contains*** O. fracticomis ***and*** O. similis.

| Kaiserstuhl | Sierra Nevada |
|---|---|
| ***Onthophagus ovatus*** | ***Onthophagus ruficapillus*** |
| ***Aphodius rufus*** | ***Aphodius castaneus*** |
| ***Aphodius*** subgenus ***Chilothorax*** | ***Aphodius*** subgenus ***Melinopterus*** |
| ***Onthophagus vacca*** | ***Onthophagus vacca*** |
| ***Onthophagus fracticornis s.l.*** | ***Onthophagus similis*** |
| ***Aphodius fimetarius*** | ***Aphodius fimetarius*** and ***foetidus*** |

Most cold temperate Scarabaeidea produce only one generation per year (CAMBEFORT & HANSKI, 1991), although they possess the physiological capacity to reproduce more often per year (LANDIN, 1961; YASUDA, 1987). Half of the northern European Aphodiinae hibernate in the adult state, 10-20% as 3rd instar larvae, another quarter is polymorphic and hibernates as adults or 3rd instar. In some species the eggs is the hibernation state (LANDIN, 1961). Polymodal patterns in the seasonal occurrence of species indicate an intraspecific variability in hibernation state: adult beetles, 3rd instar and sometimes the eggs hibernate (HANSKI, 1980). This polymorphism may result in overlapping generations, each of which needs approximately one year for a complete life cycle (the ontogenesis from the egg to the adult takes only 1-2 months, but the emergence of adults is postponed).

Overlapping generations make it more difficult to recognize a species to be bivoltine. *Onthophagus verticicornis, Aphodius haemorrhoidalis, A. pusillus* and *A. granarius* (fig. 7, 9 & 12) are examples in my study, which show a very dense bimodal pattern with only a small intermediate minimum between the two peaks. With the exception of *O. verticicornis* a bivoltine characteristic of these species has already been discussed by some authors (LANDIN, 1961; HOLTER, 1982). If these species were truly bivoltine, they would have an extremely rapid development from the egg to the reproductive adult. In all studies so far *Aphodius paykulli, A. distinctus, A. prodromus* and *A. sphacelatus* (fig. 8 & 13) are clearly bimodal species forming another group in which voltinity is controversially discussed by the same authors (LANDIN, 1961; HOLTER, 1982). If sampling of specimens is continuously carried out during the winter months, *A. paykulli* shows a clear unimodal pattern and is the only extreme winter specialist at the Schelinger Pasture. In contrast to Southern Sweden, where this species hibernates in the egg state (LANDIN, 1961), the predominant hibernation state at the Kaiserstuhl seems to be the adult. The closely related species *A. distinctus* shows a clear bimodality. While this species does not indicate bivoltinity, *A. prodromus* and *A. sphacelatus* show their maxima in early spring, indicating that the majority of the population hibernated in the egg state and not in the adult state. The availability and reliability of winter and early spring dung resources at the Kaiserstuhl site might be the ultimate factors of this difference. A lot of confusion about the question of voltinity appears, because one author counts the number of generations which appear throughout the year, while others count the number of new generations per year. Bimodal Scarabaeidae with an adult hibernation state *(Onthophagus vacca, O. coenobita, O. ovatus, O. fracticornis, Aphodius prodromus* and *A. pusillus* - fig. 6, 8, 9, 10 & 12) show two generations per year, the hibernating autumn generation of the previous year and the new generation, which will hibernate in that year.

Besides this intraspecific polymorphism in the "seasonal phenotype" (HANSKI, 1980) of the same geographic latitude, there might be a latitudinal gradient in the state of diapause and number of new generations per year. The best example is *Aphodius fimetarius,* which hibernates in northern latitudes in the adult state and shows only one generation in the high north and two in southern Sweden (LANDIN, 1961), but is known to hibernate in all developmental stages in Germany (SCHMIDT, 1935). The polymodal seasonal distribution pattern might even indicate trivoltinity at the Kaiserstuhl and the same in the Sierra Nevada (AVILA & PASCUAL, 1988fo). The presence of adult *Aphodius rufus* in December indicates a tendency to hibernate in this state and not only as 3rd instar as in Scandinavia.

Little is known on the phenology and voltinity of Hydrophilidae. *Shaeridium* and *Cercyon* both have very short larval developments *(Sphaeridium* approx. 30

days, HOI.TER, pers. com.; *Cercyon* 21-33,5 days in the laboratory, SCHULTE, 1985), so they might be able to produce numerous overlapping generations each year. On the other hand, some Hydrophilidae show similar phenological distribution patterns in Belgium (DE GRAEF & DESIERE, 1984), southern England (HANSKI, 1980) and the Kaiserstuhl, so there might be a fixed pattern for these species. LAURENCE (1954) found larvae of Hydrophilidae throughout the winter in cow pats, nevertheless they were in much smaller numbers than between April and August. *Cercyon quisquilius* is found to hibernate as an adult (MOHR, 1943). At the Kaiserstuhl this species was the only Hydrophilidae to be well represented in winter. C. *haemorrhoidalis*, *C. lugubris* and *C. pygmaeus* were abundant at the beginning of December, but compared with the other months of their seasonal occurrence they were quite rare. Maybe their presence is restricted to mild winter climate, which was true for the first December sample. *C. lateralis*, a medium size *Cercyon-species*, which shows the longest ontogenesis beyond *Cercyon* (33.5 days, SCHULTE, 1985), is the only species to show a unimodal pattern, while all the other Hydrophilidae show at least bi- or trimodality.

On Dec, 29th, the most extreme winter day (permanent frost between Dec, 26th and Jan, 5th, daily average -6.1°C), three specimens of *Aphodius paykulli* were the only living beetles to be found between the frozen ground and a frozen cow pat. As mentioned above, some species of the subgenus *Chilothorax* seem to be especially resistant against cold and frost followed by some *Melinopterus* species and the winter generations of multivoltine seasonal generalists *Aphodius fimetarius* and *Onthophagus fracticornis* s.l. (AVILA & PASCUAL, 1988&)- Due to the predominance of the paracoprid way of life, in warm temperate pasture biotops, winter is the only season for Aphodiinae to dominate (LUMARET & KIRK, 1991). During winter the dominance of Aphodiinae at the Kaiserstuhl is nearly exclusive, whereas their proportion declines to 51.6% in the summer, which is in accordance with the biogeographical position of the site between typical warm and cold temperate climates.

Specialisation during less attractive and therefore less competitive winter months needs either physiological predispositions or special behavioural strategies or both. Winter and summer generations of *Aphodius fimetarius* show different tolerance of cold temperatures. First mobility of cold specimens occurred at -1°C in winter and +6.4°C in summer beetles, whereas the summer generation showed more tolerance for high temperatures (LANDIN, 1961). For a dung dwelling beetle, a behavioural strategy is to search for suitable microclimatic conditions, as it is the case for *Aphodius paykulli* or for a paracoprid species to dig very deep into the soil in order to reach below the level of frozen soil, which was true for *Geotrupes spiniger,* which digs deeper than 30 cm.

As I was able to show in another study on a sheep pasture near Freiburg (SW-Germany) (WASSMER, 1991), there is not only a qualitative, but also a quantitative phenological separation in the biomass of dung beetle species, especially for *Aphodius.* Although according to GAUSE'S principle (GAUSE, 1934) closely related species should not cooccur, within *Aphodius* mean pair niche overlaps of species during the sampling months were significantly lower than between *Aphodius* and other genera, whereas the opposite was true for *Onthophagus* and *Sphaeridium* (table 1). These findings might be due to an extreme competition for suitable dung pats within *Aphodius.* Competition should be more exclusive for dung dwelling species than for paracoprid species, because the total amount of dung is not the limiting factor, but the amount of suitable dung pats in terms of their microclimate. There are many reports on severe interference competition among *Aphodius* larvae (e. g. MADLE, 1934; STEVENSON & DINDAL, 1985). Therefore differences in phenology and body size seem to be more suitable than microhabitat factors in order to avoid this kind of competition. The differences between *Aphodius* and the likewise dung dwelling Hydrophilidae might be due to the shorter life cycle of the latter and the fact that Hydrophilid larvae are not coprophagous.

In a recent study LUMARET *et al.* (1992) found an increase by a factor of three in beetle numbers and a 2.5-fold increase in beetle biomass after dung resources were increased by the factor 3 shifting from sheep to cow grazing at the Languedoc. Relative frequency of dwellers increases from 40.6 % to 82.7 %, while tunnelers and rollers became more rare. These findings could be based on two factors: 1. the total amount of dung increased and 2. the shift from sheep to cattle grazing provides dung with much better microclimatic conditions for dung dwelling species. Competition between dung dwelling species might be harder in dry and warm climate and on extensive pastures, where only sheep or hardy small cattle find enough to eat. In northern European pastures, resource shortages are not believed to be an important factor on anthropogenic pasture biotopes (LANDIN, 1961; HOLTER, 1982; HANSKI, 1987). Contrary to the conditions of this study as well as in LUMARET *et al.* (1992), the amount of cow pats on intensive pastures in cold temperate regions is much higher and the microclimatic situation within the dung is more favourable.

Results suggest that phenological diversity within dung dwelling *Aphodius* could be a major reason why there are so many sympatric species within this genus. Because the patterns of phenological distribution of species were confirmed by a great number of studies from different geographic locations (see Introduction), it seems reasonable to accept the presence of genetically fixed phenologies. Whether the quantitative phenological segregation of species is a result of actual competition, or fixed genetic patterns within the species remains to be proved by studies which manipulate dominance structures artificially.

The coexistence of many paracoprid beetles as well as coprophagous Hydrophilidae and Staphylinidae should be facilitated mainly by other niche dimensions (e. g. dropping size and water content of the dung pats, SOWIG & WASSMER, 1994).

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## APPENDIX

Occurrence (Abundance) of the 52 species of the dung beetles community at the Kaiserstuhl. Three species pairs of *Onthophagus* could not be separated quantitatively. Nomenclature and systematics according to KRELL & FERY (1992) and VOGT (1971).

*Geotrupidae*

| | |
|---|---|
| Geotrupes stercorarius | 2 |
| Geotrupes spiniger | 23 |

*Scarabaeidae*

| | |
|---|---|
| Euoniticellus fulvus | 2 |
| Copris lunaris | 79 |
| Onthophagus taurus | Qualitatively |
| Onthophagus illyricus | Qualitatively |
| Onthophagus taurus s.l. | 556 |
| Onthophagus verticicornis | 422 |
| Onthophagus ovatus | Qualitatively |
| Onthophagus joannae | Qualitatively |
| Onthophagus ovatus s.l. | 2606 |
| Onthophagus vacca | 2975 |
| Onthophagus fracticornis | Qualitatively |
| Onthophagus similis | Qualitatively |
| Onthophagus fracticornis s.l. | 3363 |
| Onthophagus coenobita | 75 |
| Oxyomus silvestris | 2232 |
| Aphodius subterraneus | 1 |
| Aphodius scrutator | 4 |
| Aphodius fossor | 76 |
| Aphodius haemorrhoidalis | 1218 |
| Aphodius arenarius | 185 |
| Aphodius rufipes | 448 |
| Aphodius luridus | 7 |
| Aphodius maculatus | 3 |
| Aphodius zenkeri | 4 |
| Aphodius pusillus | 3362 |
| Aphodius biguttatus | 202 |
| Aphodius sticticus | 2651 |
| Aphodius distinctus | 645 |
| Aphodius paykulli | 1421 |
| Aphodius contaminatus | 2 |
| Aphodius sphacelatus | 319 |
| Aphodius prodromus | 3443 |
| Aphodius fimetarius | 3501 |
| Aphodius foetens | 67 |
| Aphodius ater | 4 |
| Aphodius rufus | 2776 |
| Aphodius granarius | 2590 |
| Rhyssemus germanus | 2 |
| Maladera holosericea | 2 |

*Hydrophilidae*

| | |
|---|---|
| Sphaeridium bipustulatum | 558 |
| Sphaeridium scarabaeoides | 751 |
| Sphaeridium lunatum | 1253 |
| Cercyon lugubris | 33 |
| Cercyon impressus | 22 |
| Cercyon haemorrhoidalis | 1005 |
| Cercyon melanocephalus | 12 |
| Cercyon lateralis | 36 |
| Cercyon laminatus | 1 |
| Cercyon unipunctatus | 3 |
| Cercyon quisquilius | 171 |
| Cercyon terminatus | 25 |
| Cercyon pygmaeus | 533 |
| Cryptopleurum minutum | 622 |