

Spatial separation of Afrotropical dung beetle guilds: a trade-off between competitive superiority and energetic constraints (Coleoptera: Scarabaeidae)

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In the forest-savanna mosaic of Côte d'Ivoire (Parc National de la Comoé), we studied the guild structure of dung beetle assemblages of fresh buffalo faeces (60 samples, 19 626 specimens) in three adjacent habitats: savanna parkland, gallery forest, grassland of the river valley. We found clear patterns at the guild level determined by the habitat type and time of day: in the savanna parkland during the day, telecoprids (rollers) and their kleptoparasites are dominant. At night, paracoprids (tunnelers) and endocoprids (dwellers) dominate the dung beetle assemblages. In the river valley during the day and the gallery forest all day and night, the abundance of dung beetles is very low and does not reach a competitive level. In the river valley at night, endocoprids are quite abundant. Abundances of kleptoparasites and their hosts are positively correlated. The telecoprids are the most competitively superior guild since they use the resource most rapidly, but their abundance is correlated with temperature of faeces and soil. This is probably because their mode of resource utilization is energetically costly, so they require higher temperatures in order to maximize their competitiveness. Their ecological tolerance is therefore narrow and they are only present in the savanna parkland during the day. The endocoprids are the least competitive guild, since they do not relocate the resource and so are not able to monopolize parts of it. However, their mode of resource utilization is less energetically costly. They seem to be more tolerant of temperature fluctuation and more able to cross barriers such as the gallery forest. Spatial separation of Afrotropical dung beetle guilds is likely to be due to a trade-off between competitive superiority and energetic constraints.

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Coprophagous scarab beetles use their substrate in different ways, by which they are classified into guilds (Bornemissza 1969, Cambefort and Hanski 1991). Species of the roller guild (telecoprids) rapidly form balls from the faeces, roll them away from the food source and deposit them in or on the soil to ensure the exclusive use of this part of the resource. Formation of a ball generally takes much less than one hour, in small

Sisyphini only a few minutes (Halfpter and Matthews 1966: 103, Doube 1990, unpubl.). The tunnelers (paracoprids) burrow tunnels to make nests directly under the food source and bring dung into the nest where they form dung balls. This is relatively time-consuming and takes at least six hours (Doube 1990). Dwellers (endocoprids) feed and reproduce directly in the dung pat. Kleptoparasites use the faeces portions monopolized by

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species of other guilds. They penetrate dung balls made by telecoprids or the dung mass in the subterranean nests of paracoprids.

If the beetles of all guilds are abundant, these modes of resource utilisation are mutually exclusive, with a hierarchy of competitive superiority: when the substrate is rolled away by rapid telecoprids, paracoprids have nothing left to bury. When the substrate is rolled away or buried, the endocoprids have nothing to lay their eggs in. The competitively superior species are therefore the fast telecoprids, the least competitive species are the endocoprids (Doube 1990). The success of kleptoparasites depends largely on the success of their hosts. Dung relocation (rolling and tunnelling) is burdened with high energetic costs whereas endocoprid behaviour and kleptoparasitism is much less energetically costly.

Success of any species in occupying any vacancy in the biocenosis is determined mostly by its early presence or arrival, especially if species are able to monopolize a part or the resource – “first come first served” (e.g. Tokeshi 1999: 308). In many dung beetle assemblages, this priority principle is prevalent (Hanski 1989). In our project we investigated whether competitively inferior guilds have evolved mechanisms for avoiding competition, or whether they depend on random success to coexist with superior competitors.

Habitat heterogeneity is thought to be one of the parameters determining species diversity at a regional scale (Huston 1994: 40, Rosenzweig 1995: 32, Begon et al. 1996: 894) and perhaps the most important one (Schoener 1974). The objective of the present study was to find out if competitively inferior dung beetle guilds use the habitat heterogeneity to coexist locally with superior competitors. In the middle of the rainy season when the abundance of dung beetles is generally high, we compare the coprocenoses of fresh buffalo dung in different adjacent habitats (savanna parkland, the gallery forest and the grassland strip in the river valley). These habitat types are more or less continuous and adjoin each other (the river valley is separated from the savanna by the gallery forest). They comprise an important part of the habitat heterogeneity of the study area. We found spatial and diel separation at guild level and try to explain why the competitively superior guild (telecoprids) does not dominate all dung beetle assemblages.

Material and methods

Study area

We conducted our experiments in the southern part of the Parc National de la Comoé in north-eastern Ivory Coast, West Africa around the research camp of the Univ. of Würzburg (Lola-Camp). The study site is at the border between the Guinea and Subsudan savanna

attributed by Porembski (1991) to the former and by Poilecot (1991), amongst others, to the latter. White (1983) called this region the Guineo-Congolian mosaic of lowland rain forest and secondary grassland. It is generally considered to be a secondary man-made but long established landscape (White 1983, Kadomura 1989, Poilecot 1991: 40, Anhuf 1997).

In the forest-savanna mosaic of the western Afrotropics, some different habitat types occur in the immediate vicinity of each other. A matrix of different savanna types contains discrete patches of forest habitats with abrupt borders, such as gallery forests and forest islands. This ecotone exists over virtually all of the West and Central African forest-savanna border (Kadomura 1989). It was described, for instance, from our study area, the Parc National de la Comoé (Hovestadt et al. 1999), from the V-Baoulé in central Côte d'Ivoire (Anhuf 1997: 16) and from west-central Ghana (Swaine et al. 1976), or, conversely, as a forest with savanna islands, from south-western Nigeria (Adejwon and Adesina 1992).

In the study area, the savanna parkland takes up the largest area. Within the savanna, we find forest islands of different types. Continuous gallery forests exist along rivers that generally have running water for > 6 months. Between the gallery forest and the river itself, a small strip of grassland may be present as long as the river has not reached its highest level. The soil in the study area is of ferrallitic type (medium to slightly desaturated) (Perraud 1971).

The dung beetle fauna in the study area is rich and abundant during the rainy season. Cambefort recorded 132 sympatric dung beetle species not counting the endocoprid Aphodiinae (Hanski and Cambefort 1991a). In the course of our project on coprocenoses and necrocenoses in the Ivory Coast, we found several additional species in the same area.

Study sites

We chose a locality (Fig. 1), where three different habitats adjoin: 1) grassland of the river valley, soil mostly not deeper than 10 cm, rocky (Fig. 2); sample site: 3°49'02"W, 8°45'13"N. 2) Continuous gallery forest of the drier type (Fig. 3), never flooded, nor burned; sample site: 3°48'57"W, 8°45'10"N. 3) Savanna parkland (“savane arbustive” after Poilecot 1991: 31; bushes and trees not higher than 8 m), annually burned (Fig. 4); sample site: 3°48'58"W, 8°45'02"N. All the sites are within a 1 km square. Since dung beetles can fly > 1 km to forage (Paik 1976: 167, Hanski 1980, Roslin 2000), most of colonizing beetles probably came from outside the study area, which is to be considered an open system. Therefore, strong reciprocal influences of simultaneously exposed dung pats are unlikely.

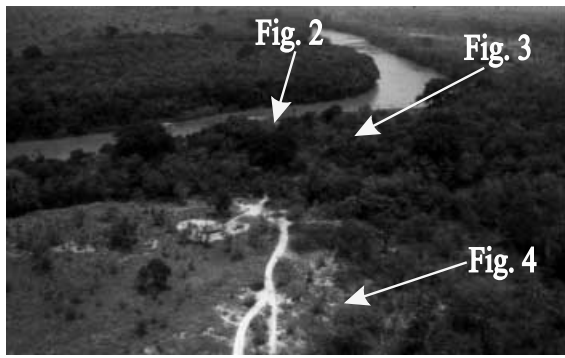


Fig. 1. Aerial view of the study area around the Lola-Camp at the Comoé river, Parc National de la Comoé, Côte d'Ivoire. Arrows: sample sites, as shown in Figs 2–4. Photo: F. Fischer.



Fig. 2. Sample site in the Comoé river valley (grassland).



Fig. 3. Sample site in the Comoé gallery forest around the Lola-Camp.

We did not consider forest islands because we wanted to determine the influence of habitat heterogeneity on the diversity of coprophagous beetles and avoid interference with fragmentation effects. Hence, we studied only sufficiently large, continuous habitats.

Extensive edge effects are known to occur in tropical forest habitats. Microclimatic and soil moisture edge effects may extend >200 m into the forest (Didham and Lawton 1999). Since the gallery forest



Fig. 4. Sample site in the savanna parkland near the Lola-Camp.

has a maximum width of 300 m on each side of the river (Anon. 1979: 58) and is mostly not broader than 200 m, this habitat as a whole can be considered as an edge. However, we avoided the very edge of the forest.

If our site is to act as a model for habitat preferences of dung beetles in savanna ecotones, then its spatial heterogeneity must have been established a long time ago, so that the structure of the coprocenoses is no longer dominated by dispersal processes. These requirements are met, since the mosaic landscape pattern of the forest-savanna border in the Côte d'Ivoire was already established in pre-colonial times (Wohlfarth-Bottermann 1994: 373). In West Africa, savannization caused by human impact has been prevalent for at least 1000 yr (Anhuf 1997). This is probably long enough to preclude that dispersal processes still influence the structure of present coprocenoses to a major extent, because dung beetles disperse rapidly (as shown, e.g. in the afro-tropical *Digitonthophagus gazella* (Fabricius) after release in North America [43–808 km yr⁻¹; Barbero and López-Guerrero 1992]).

Microclimatic characterization of habitats and sample sites

To identify microclimatic differences between the habitats, we measured 1) air temperature at ca 1 m above ground at start and end of the exposure period, 2) soil temperature at a depth of 1 cm and 10 cm at start and end of the exposure period (10 cm was not possible in the river valley because of thin soil layer), 3) dung temperature just before collecting the sample, and 4) volumetric humidity of the uppermost 10 cm of the soil (not possible in the river valley) at start and end of the exposure period (1–3: Microcomputer thermocouple thermometer HI9063, Hanna Instruments; 4: TDR device Trime FM2 with probe P2, Imko, Ettlingen, Germany).

Experiments

From 9 to 25 July 1997 (drier period within the rainy season: "Little Dry Season" [Ojo 1977: 97]) we deposited 20 portions of 1 kg (900 ml) fresh faeces of buffalo (*Syncerus caffer* (Sparrman), Bovidae) on the soil in each of the three habitats. Ten of them were deposited from 6:00 to 16:00 h, ten others from 18:00 to 6:00 h, because the flight activity of dung beetles differs strongly between night and day at the guild level. Therefore, coprocenoses of freshly exposed substrate differ according to exposure (Westerwalbesloh et al. 1998). We exposed simultaneously a maximum of two portions per site per time and always the same number of samples in each habitat. The samples that were exposed during the day were collected after only 10 h since, after 16:00 h, the number of diurnal beetles in dung pats decreases. After the exposure period the faeces and soil beneath, that was populated by coprophagous beetles were floated in a bucket of water (Roberts 1884). In addition, we searched the complete sediment in the bucket for remaining beetles. Moore's (1954) often cited refinement (holding the dung mass down in the bucket by a mesh wire screen) is inadvisable since not all beetles leave the substrate of their own accord. For quantitative records it is essential to stir the dung mass thoroughly several times and to search the sediment carefully afterwards (Rougon and Rougon 1979). In the sediment, we regularly found *Sisyphus*, *Tiniocellus*, *Drepanocerus*, Aphodiinae, and a high proportion of the *Pedaria*.

For our experiments we used fresh dung since, in the study area, old buffalo dung is virtually absent in the savanna during the first half of the rainy season. The pats we exposed were artificially formed, but Barth et al. (1994) showed that the coprocenoses of artificially formed and naturally voided dung pats do not differ significantly. The flight activity of dung beetles is strongly influenced by weather conditions, especially by rainfall (Walter 1985, unpubl.). Since the rainfall was constantly low during our study period (2 mm on 12 July and 11 mm on 15 July) and just after the latter rainfall event we did not run our experiments, this variation is not likely to affect our results strongly.

Since in natural tropical habitats the first dung beetles arrive at the dung less than one minute after deposition, it is impossible to find uncolonised fresh dung. Therefore, we had to extract all beetles from the substrate by hand before starting our experiments. Even with the utmost care, this method does not ensure that every beetle is removed, especially tiny *Cleptocaccobius* or some Sisyphini, which are often completely covered with faeces. However, given the mostly large number of beetles received per sample, any error resulting from single specimens that were overlooked before the exposure is likely to be negligible.

We used faeces of buffalo, since this species has a reasonable population in the study area. The population in the Parc National de la Comoé is estimated at between 3000 (Lauginie 1995: 243) and 8200 individuals (Fischer and Linsenmair 2001). Its distribution centre coincides with the study area in the south-eastern part of the park (Steinhauer-Burkart 1987). Moreover, buffaloes are presumably still present in most parts of the Ivory Coast, as they were 15 yr before our study (Roth and Hoppe-Dominik 1987). Therefore, our bait is not a regional speciality but a common resource in the region.

We did not use traps because we wanted to record established coprocenoses after a fixed period of exposure of the resource, not all of the beetles visiting the resource during a period of time. Some beetles may approach the dung pat but fly away after a short exploration (unpubl.) or when the pat is already highly populated (Landin 1961: 207). With our method we register only the actual users of a resource whereas traps collect both users and tourists. In a comparative study, Lobo et al. (1988) demonstrated that baited pitfall traps contain a much larger number of individuals than the same amount of dung exposed on the soil surface. Traps overestimate the portion of some groups containing many tourists. These groups cannot be unambiguously identified among the trapped beetles. Moreover with the condensed succession (Walter 1980) that we find in tropical ecosystems, the condition and, hence, the attractive effect of the bait in a trap develops differently from a bait exposed on soil in natural condition, even in a short period of time. However, with our method we underestimated the proportion of telecoprids in the coprocenoses since many of them have already left the pat before we collected the sample. We tried to reduce this bias by scheduling our sampling during the activity period of the telecoprids. Although we obviously got a biased pattern, we are able to identify the bias, whereas in pitfall trap sampling the overestimated groups are not recognizable.

The collected material is deposited in the The Natural History Museum, London.

Guild classification

We treat every species as belonging to exactly one guild. The term guilds is used in its original definition as group of species which use the same resource in a similar way regardless of their phylogenetic relationship (Root 1967, Simberloff and Dayan 1991). However, we confine this analysis to dung beetles of the family Scarabaeidae since they are the major users of the dung resource. Other coprophilous beetles (Histeridae, Hydrophilidae, Carabidae, Staphylinidae) are either predators or occur in relatively low numbers. We follow the rough classification of coprophagous members of the

coprocenosis into the guilds of telecoprids (rollers), paracoprids (tunnelers), endocoprids (dwellers) and kleptoparasites (Bornemissza 1969, Cambefort and Hanski 1991), but we divide the last group into kleptoparasites of paracoprids and those of telecoprids (Cambefort 1991: 164). As usual, there is no simple correlation between higher taxa and guilds. In the studied cenoses, the guilds consist of the following members: 1) telecoprids (rollers): all Gymnopleurini, all Sisyphini (Scarabaeini are not present in our samples); 2) paracoprids (tunnelers): all Coprini (incl. Dichotomini, see Montreuil 1998), all Onitini, all Oniticellini (except *Oniticellus formosus* Chevrolat), all Onthophagini (except for the species listed under kleptoparasites), *Aphodius (Neocolobopterus) maculicollis* Reiche, which burrows short ducts into the soil under the dung pat (unpubl.); 3) endocoprids (dwellers): all Aphodiinae (except *Aphodius maculicollis*), *Oniticellus formosus* (Davis 1989); 4) obligatory kleptoparasites (Cambefort 1984): a) of paracoprids: *Pedaria* spp., *Onthophagus juvenicus* Klug; b) of telecoprids: *Cleptocaccobius* spp., *Hyalonthophagus nigroviolaceus* d'Orbigny, *Onthophagus lioides* d'Orbigny, *O. tersipennis* d'Orbigny.

Many other species of paracoprids and endocoprids may be facultatively kleptoparasitic (Cambefort 1984, unpubl.). Since they usually have modes of resource exploitation other than kleptoparasitism, they are not considered as kleptoparasites here.

Some Aphodiinae are known to lay their eggs in the ground beneath the dung pat and are therefore not endocoprids in the strict sense (Yoshida and Katakura 1992, Vitner 1998). Moreover the larvae of some species develop not in dung but facultatively or obligatorily in detritus or humus (Vlug and Dreteler 1994, Gittings and Giller 1997) or even feed on subterranean parts of plants (Jerath and Ritcher 1959) but their adults are usually coprophagous. However, the reproductive biology of the West African Aphodiinae is virtually unknown. From the species in our samples, only *Aphodius maculicollis* has been identified to be paracoprid. Since the Aphodiinae that we found had remained in the dung pat for a few hours they are obviously able to use the substrate at least to feed themselves and are, therefore, all considered to be endocoprids (except *A. maculicollis*) even if reproductive activity within the dung pat could not be proven.

F.-T. K. identified the specimens.

Statistics

For the statistical analyses we used Canoco for Windows 4.0 (Centre for Biometry Wageningen, The Netherlands), SsS 1.1a (Rubisoft Software), XLSTAT 4.4 (Thierry Fahmy), and STATISTICA 5.5 (StatSoft).

Since the data sets of microclimatic parameters are not independent, we used the Friedman test to check if at least one of the medians of the data sets is different from any other. Then we tested pairwise difference using the test of Dunn (SsS, Horn and Vollandt 1995). In cases with only one pair of data sets, we used the Wilcoxon matched pairs test (Statistica).

Correlations between the abundance of guilds are shown with a standardized principal component analysis (PCA) (Canoco) using log transformed guild abundance data. PCA requires a normal distribution which is not present in all our data, even when log transformed (telecoprids and both groups of kleptoparasites; Kolmogoroff-Smirnoff test, SsS), but for merely descriptive purposes, larger departures from ideal data structure are tolerable (Greig-Smith 1980, Gauch 1982: 137). Significance of the correlations is tested with the non-parametric Spearman rank correlation coefficient (XLSTAT) using the critical values given by Zar (1996: App115).

A standardized redundancy analysis (RDA) (Canoco, Jongman et al. 1995, Legendre and Legendre 1998) using log transformed guild abundance data shows the relationship between environmental parameters and guild abundances. Daytimes and habitats are coded as separate variables. The highest increase of temperature was rescaled to 0, the highest decrease becomes the highest value.

Results

Differences of the guild structure between habitats

The total number of specimens according to guild and habitat are given in Table 1 (day and night samples pooled). In the open habitats (savanna and river valley), the absolute number of dung beetles is ca 10 times higher than in the dense gallery forest. We find one by far dominant group in each habitat: endocoprids in the river valley and in the gallery forest and kleptoparasites of telecoprids in the savanna. In the river valley, no other abundant group is present. In the gallery forest paracoprids make up a large portion of the dung beetle fauna, in the savanna telecoprids and paracoprids.

Since the structure of coprocenoses differs strongly between night and day (Westerwalbesloh et al. 1998), pooling the data from the night and day samples gives an unrealistic picture of the dung beetle assemblages with high variances. The dominant guild in the most spacious habitat (savanna) during the day are the kleptoparasites of telecoprids (54%), followed by their hosts, the telecoprids (26%). Endocoprids are negligible during daytime (1%) but are one of the two dominant groups at night (45%), together with the paracoprids (48%) (Fig. 5). The kleptoparasites of the paracoprids have their highest overall abundance in the savanna at

Table 1. Proportion of guilds in dung beetle faunas of different habitats; pooled numbers of 20 samples each (10 day/10 night samples). The last row shows the number of dung beetles per habitat and its proportion of the overall number of dung beetles that we obtained in our experiment.

Habitat	River valley (grassland)		Gallery forest		Savanna	
	Individuals	%	Individuals	%	Individuals	%
Telecoprids	5	0.06	16	1.80	2301	20.83
Paracoprids	306	3.98	329	37.05	2751	24.91
Endocoprids	7312	95.05	530	59.68	1062	9.62
Klepto. of Tele.	69	0.90	11	1.24	4784	43.31
Klepto. of Para.	1	0.01	2	0.23	147	1.33
Total (n = 19 626)	7693	≅ 39.2	888	≅ 4.5	11 045	≅ 56.3

night (Table 2), but their proportion of the coprocenosis is low (6%). At night, telecoprids and their kleptoparasites are rare in all habitats. In the gallery forest, the abundance of dung beetles in buffalo dung is low (22 ± 8 individuals/kg dung; at night 66 ± 38 ind. kg^{-1} dung). They certainly occur at a non-competitive level. Most of the diurnal forest dung beetles are paracoprids (74%), at night the endocoprids are dominant (73%), followed by the paracoprids (25%). In the river valley during the day, the low number of beetles and the high variance in the proportions of the guilds does not allow us to trace any patterns except for the virtual absence of telecoprids (1%). At night, however, the coprocenoses in the river valley showed the second highest overall abundance: 749 ± 451 ind. kg^{-1} dung. The buffalo dung there is nearly exclusively populated by masses of tiny Aphodiinae (endocoprids) (97%) and a few paracoprids (3%).

Correlation of guilds

The PCA (Fig. 6) shows graphically the correlations of guilds. Paracoprids and their kleptoparasites, and telecoprids and their kleptoparasites are positively correlated, respectively (Spearman rank correlation coefficients 0.66 and 0.77; $p \leq 0.01$). The vectors for the endocoprids and the telecoprids, however, are nearly perpendicular. These last two guilds show only a slightly negative correlation which is not statistically significant (-0.18 ; $p > 0.1$). However, there is a highly significant negative correlation between the endocoprids and the kleptoparasites of telecoprids (-0.34 ; $p \leq 0.01$). Since the telecoprids are underestimated in our samples, a significantly negative correlation between endocoprids and telecoprids is possibly present.

Guild structure and environmental variables

The microclimatic parameters of the three habitats are given in Table 3. The change of the air temperature during the experimental period of 10 h during the day is significantly higher in the open habitats than in the

forest. During the night, this change does not differ between the habitats. The soil temperature and its change during the experiments at a depth of 1 cm in the gallery forest differs significantly from the open habitats. Particularly during the day, the difference is much smaller in the forest. Even at 10 cm depth, the warming during the day and the cooling during the night is much greater in the savanna than in the gallery forest ($p < 0.01$). The soil humidity, however, is not significantly different in these habitats. Faeces exposed in the morning in the open habitats are ca 6 degrees warmer in the evening than those exposed in the forest. The dung exposed in the evening in the river valley is only slightly colder the next morning than the dung in the savanna, even if this difference is statistically significant. In summary, the temperature changes of the soil and faeces are much greater in the open habitats than in the forest. The diurnal temperature of soil and faeces in the open habitats is higher.

Relationships between environmental parameters and guild abundances are shown by an RDA (Fig. 7). There is a clear overall difference between the assemblages of day and night and of savanna and gallery forest/river valley. Telecoprids and paracoprids as well as both groups of kleptoparasites are strongly associated with the savanna and show mainly diurnal activity whereas endocoprids are active at night and are found instead in the river valley and the gallery forest. Abundance of telecoprids and their kleptoparasites are significantly correlated with the temperature of the faeces and to the soil temperature at the end of the experiments, less so with the air temperature at the end of the experiments. The number of paracoprids is less strongly correlated with the faeces temperature. The abundance of endocoprids, however, is correlated with the initial air and soil temperature and to the differences (i.e. decreases) of soil and air temperature during the experiment.

Most of the environmental variables are potentially relevant for the interpretation of guild patterns since their eigenvalues in the RDA are > 0.2 (Table 4). Even the temperature of the faeces with an eigenvalue of only 0.15 has a significant conditional effect ($p = 0.008$) in the interplay of all variables (Table 4). The most important parameters for the guild structure are the differ-

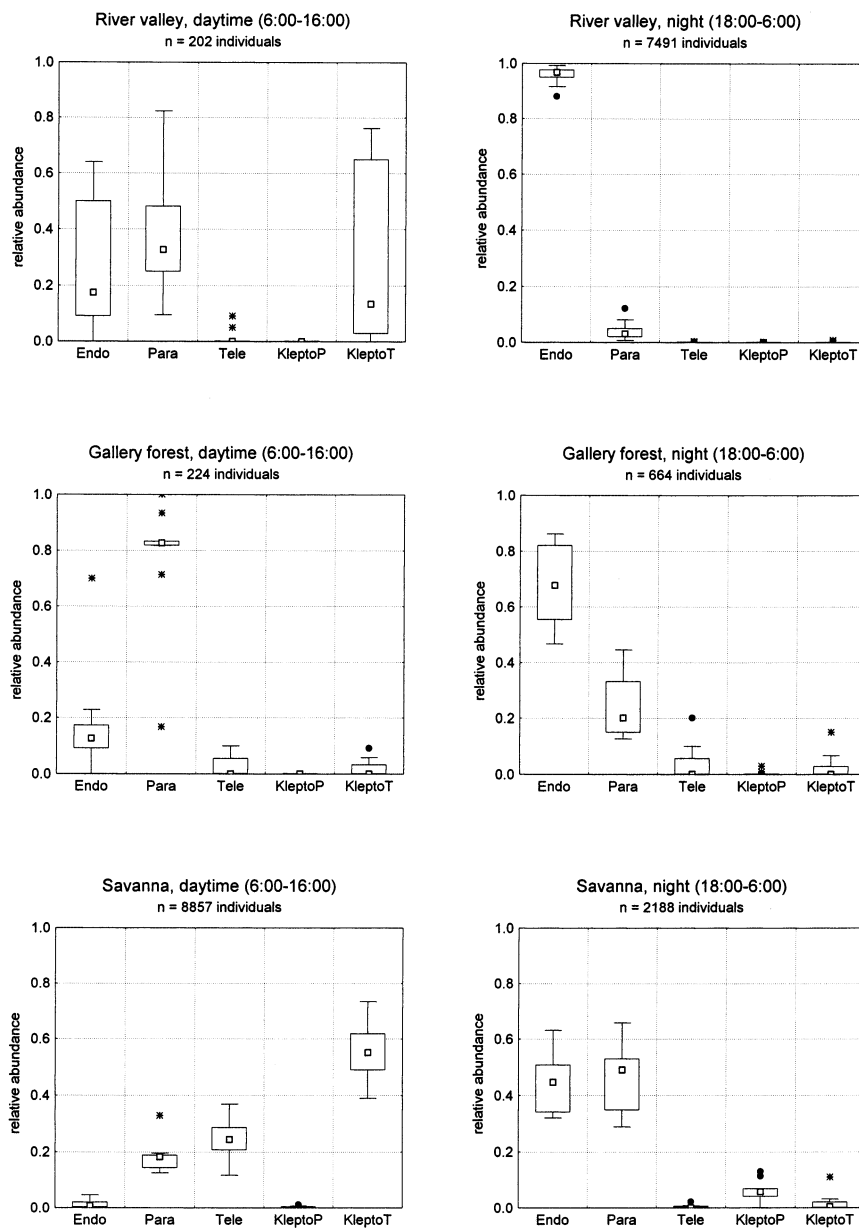


Fig. 5. Guild structure of coprocenoses in three habitats (savanna, gallery forest, grassland of river valley) at daytime and at night. Box-Whisker-Plots from Medians (\square) of relative abundance (percentages) of guilds, with 25%/75% quartiles (rectangle), minimum/maximum values (bar), outliers (\bullet) and extremes (*). Endo = endocoprids (dwellers), KleptoT = kleptoparasites of telecoprids. KleptoP = kleptoparasites of paracoprids. Tele = telecoprids (rollers). Para = paracoprids (tunnelers).

ence between soil temperature (1 cm depth) at start and at the end of the experiment and the savanna as a habitat. The changes in soil temperature are significantly different between the gallery forest and open habitats during the day (Dunn test, $p < 0.01$) and between the savanna and gallery forest at night ($p < 0.01$).

Discussion

Abundance and competition

In different adjacent habitats abundance and guild structure of dung beetle assemblages clearly differ (Fig.

5). Appreciable fluctuation of guild proportions, shown by a large inter-quartile range and outlying extremes of the relative abundances (Fig. 5), is only present in those habitats and during those times of the day when the abundance of dung beetles is very low. These low abundances are far below any presumed competitive level, particularly in the river valley during the day and, to a lesser extent, in the gallery forest during both day and night (Fig. 5 and Table 1). This suggests that the habitat type determines the structure of coprocenoses of herbivore dung if competition is prevalent.

The conditions in the forest cannot drive spatial separation of dung beetle species or guilds since a high

Table 2. Proportion of guilds by habitat and time of day (individually rounded), for number of individuals see Table 1. All entries are %.

Guild/habitat		Telecoprids (n = 2322)		Paracoprids (n = 3386)		Endocoprids (n = 8904)		Klepto. of Tele. (n = 4864)		Klepto. of Para. (n = 150)	
river valley	day	0.13	Σ 0.22	2.54	Σ 9.04	0.56	Σ 82.12	1.30	Σ 1.42	0.00	Σ 0.67
	night	0.09		6.50		81.56		0.12		0.67	
gallery forest	day	0.30	Σ 0.69	4.90	Σ 9.71	0.53	Σ 5.95	0.08	Σ 0.23	0.00	Σ 1.33
	night	0.39		4.81		5.42		1.14		1.33	
savanna	day	98.79	Σ 99.10	50.50	Σ 81.24	0.91	Σ 11.93	97.76	Σ 98.36	11.33	Σ 98.00
	night	0.30		30.74		11.02		0.60		86.67	

number of individuals per unit of resource is necessary to cause competition. In the river valley at night, only the competitively most inferior guild (endocoprids) is abundant. The competitively superior guilds (telecoprids and paracoprids) are abundant at a probably competitive level in the savanna during the day and at night, respectively (Fig. 5). Hence, the savanna is the habitat where spatial separation in the competitively inferior guilds may serve as a competition avoiding strategy.

Spatial separation and aggregation of coprophagous guilds

According to the aggregation model of Atkinson and Shorrocks (1981), strong aggregation in the competitively superior species enhances the chance of survival

of the inferior species (Tokeshi 1999: 292). In our system, this model can be applied at a broader scale to guilds and habitats. The competitively superior telecoprids are aggregated in the savanna (Table 2) and predominate, together with their kleptoparasites, in the coprocenoses found there during the day (Fig. 5). At night, the telecoprids are virtually missing (corroborated by the results of a few unsystematic trapping experiments and observations). Thus, competitively inferior paracoprids and endocoprids can use the resource. The competitively most inferior endocoprids are aggregated in the river valley (Table 2) where all superior competitors are virtually absent (Fig. 5). In this way environmental diversity may not only increase the number of species but also the number of functional types (guilds) in an area, as Huston (1994: 90) stated, but how can dung beetles make use of habitat heterogeneity at guild level? Are aggregations at the guild level driven by physiological/energetic constraints, limited resources or area effects?

Influence of area size and habitat history on abundance

In the southern part of the Parc National de la Comoé the savanna takes up > 83%, the gallery forest 2.2% (Anon. 1979: 67), and the grassland of the river valley grassland < 1% of the area. Dung beetles actively accumulate at their resource. If the number of individuals present in a system depends on the area of that system (Rosenzweig 1995: 190) and a dung pat is situated in a larger habitat, it may attract a larger number of dung beetles, provided that faeces are a limited resource and that the availability of dung is not negatively correlated with the area (e.g. dung is not accumulated in the gallery forest). These assumptions are reasonable in our study since there is no evidence that the buffaloes in the Parc National de la Comoé prefer closed habitats for defecation. Therefore, we may assume that the lower abundance of beetles in the gallery forest (Table 1) is due to the smaller area of this habitat compared to the savanna parkland. Are there other possible reasons?

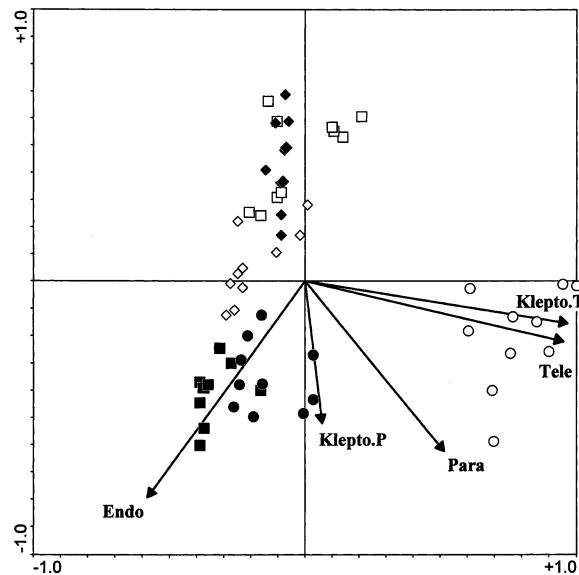


Fig. 6. Biplot of PCA of log-transformed absolute numbers of individuals within each guild (mapping of the data [samples] simultaneously with the mapping of the initial of the variables [guilds] on the factorial axes). Eigenvalues: component 1: 0.638; component 2: -0.250. ●: savanna samples; ◆: forest samples; ■: river valley samples; white: day samples, black: night samples.

Table 3. Abiotic parameters of microhabitats (arithmetic means of measurements); values separately rounded. \pm = standard deviation; n = number of measurements. In the river valley, the soil was not deep enough to measure humidity and temperature in 10 cm depth.

Habitat	River valley		Gallery forest		Savanna	
	day	night	day	night	day	night
T air start	23.7 \pm 1.2 (n = 6)	27.9 \pm 1.4 (n = 6)	22.1 \pm 1.4 (n = 6)	25.8 \pm 0.2 (n = 6)	22.2 \pm 1.6 (n = 6)	27.2 \pm 0.7 (n = 6)
T air end	29.3 \pm 1.7 (n = 6)	23.9 \pm 0.9 (n = 6)	26.6 \pm 0.6 (n = 6)	22.7 \pm 1.0 (n = 6)	28.5 \pm 1.1 (n = 6)	22.9 \pm 1.2 (n = 6)
Δ T air	+5.7 \pm 2.2 (n = 6)	-4.1 \pm 1.0 (n = 6)	+4.5 \pm 1.7 (n = 6)	-3.1 \pm 1.0 (n = 6)	+6.5 \pm 2.3 (n = 6)	-4.3 \pm 1.0 (n = 6)
T soil 1 cm start	24.9 \pm 1.0 (n = 10)	30.1 \pm 1.8 (n = 9)	23.2 \pm 0.7 (n = 10)	25.0 \pm 0.4 (n = 10)	23.9 \pm 1.2 (n = 10)	30.4 \pm 1.4 (n = 10)
T soil 1 cm end	31.3 \pm 1.8 (n = 10)	25.5 \pm 0.8 (n = 10)	24.9 \pm 0.5 (n = 10)	23.5 \pm 0.4 (n = 10)	31.3 \pm 1.8 (n = 10)	24.6 \pm 0.7 (n = 10)
Δ T soil 1 cm	+6.4 \pm 1.5 (n = 10)	-4.6 \pm 1.1 (n = 9)	+1.7 \pm 0.5 (n = 10)	-1.5 \pm 0.3 (n = 10)	+7.4 \pm 2.0 (n = 10)	-5.4 \pm 1.0 (n = 10)
T soil 10 cm start	-	-	23.7 \pm 0.4 (n = 10)	24.8 \pm 0.3 (n = 10)	24.8 \pm 1.0 (n = 10)	30.9 \pm 1.3 (n = 10)
T soil 10 cm end	-	-	24.6 \pm 0.4 (n = 10)	24.1 \pm 0.3 (n = 10)	29.5 \pm 1.2 (n = 10)	26.2 \pm 0.6 (n = 10)
Δ T soil 10 cm	-	-	+1.0 \pm 0.4 (n = 10)	-0.8 \pm 0.3 (n = 10)	+4.7 \pm 1.7 (n = 10)	-4.8 \pm 1.0 (n = 10)
H soil [vol%]	-	-	22.1 \pm 6.3 (n = 9)	22.4 \pm 6.5 (n = 10)	21.2 \pm 4.2 (n = 10)	21.8 \pm 4.7 (n = 10)
T faeces end	31.7 \pm 1.4 (n = 10)	25.2 \pm 0.6 (n = 10)	25.3 \pm 0.4 (n = 10)	24.1 \pm 0.4 (n = 9)	31.2 \pm 1.2 (n = 10)	24.8 \pm 0.5 (n = 9)

The gallery forest is likely to be a relic of a former closed forest area during the last pluvial (the Holocene altithermal 8000 BP) or even from the pluvial before ca 28 000 BP (Meave and Kellman 1994). In relatively small relic habitats, species numbers and population sizes are generally reduced. The different microclimate (Table 3), especially the much lower radiation on the soil, probably makes it difficult for thermophilous savanna species to invade and establish in these forest remnants since it requires either a complete change of autecological requirements or a vast broadening of ecological tolerance. The number of diurnal species and individuals in the gallery forest has remained at a low level. However, this is not sufficient to explain the low abundance of crepuscular and nocturnal dung beetles in the gallery forest (Table 2) because the microclimate in the savanna at night is more similar to a forest microclimate than to the microclimate in the open habitats during the daytime (Table 3). We cannot offer a satisfactory explanation for this pattern from a physiological point of view.

The abundance in the river valley (7693 ind.) is much higher than in the forest (888 ind.), mainly due to the endocoprids (Table 1), though the area is smaller. More than 80% of all collected endocoprids are from the smallest habitat (Table 2). Obviously, there is no overall correlation between habitat size and abundance of dung beetles.

The area size of a habitat type does not necessarily determine the abundance of dung beetles, but the structure of vegetation does. In open habitats many more beetles populate a dung pat. Does this preference of

open landscapes depend on the availability of resources or on physiological requirements?

Availability of herbivore dung in forest habitats

We studied dung beetles feeding on herbivore dung and used buffalo dung as bait. Buffaloes defecate randomly (Leuthold 1977: 32) and generally prefer open habitats, especially for resting. Defecation occurs during moving or resting (Mloszewski 1983: 120). Therefore, in an undisturbed environment buffalo dung is most likely to be found in open areas. However, predators, including humans, may force buffaloes to rest in more closed areas (Mloszewski 1983: 109, Mwangi and Western 1998). The traditional and still prevalent poaching in the study area certainly supports this behaviour. Geerling (1969: 6-6) more than thirty years ago found that the buffaloes in the park preferred savanna types with more vegetation. According to aerial countings of Anon. (1979: 146) 11% of all 4299 buffaloes in the Comoé Park were observed in forest habitats (12% of the area). Finally, Rödel (1996: 22) explicitly stated that buffaloes move into the gallery forests of the study area. Therefore, buffalo dung is likely to be an available resource in forest habitats. Dung of herbivores other than buffaloes is regularly to be found in gallery forests as well, especially droppings of elephants and duikers. Elephants produce coarse dung and duikers piles of small pellets, whereas buffalo faeces have a fine and homogenous texture – but generalist coprophages could use all these types of dung.

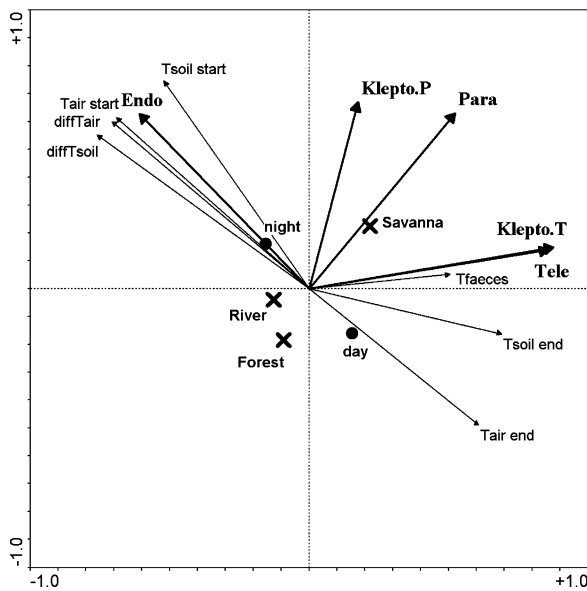


Fig. 7. RDA ordination biplot of guilds and environmental variables, based on log-transformed guild abundance data. Eigenvalues: axis 1: 0.554; axis 2: 0.188. X: centroids of sites. ●: centroids of times of the day. Endo: endocoprids (dwellers). Klepto.P.: kleptoparasites of paracoprids. Klepto.T: kleptoparasites of telecoprids. Tele: telecoprids (rollers). diffTair: difference between air temperatures at start and at the end of the experiment. diffTsoil: difference between soil temperatures (1 cm depth) at start and at the end of the experiment. Tair end: air temperature at the end of the experiment. Tair start: air temperature at start of the experiment. Tfaeces: dung temperature at the end of the experiment. Tsoil end: soil temperature (1 cm depth) at the end of the experiment. Tsoil start: soil temperature (1 cm depth) at start of the experiment.

A lack of resources is unlikely to be a major reason for the low abundance of dung beetles in gallery forests but physiological preferences or requirements might be responsible for this pattern, since the temperature of soil and air differ significantly between open and closed habitats (Table 3).

Table 4. Eigenvalues of the environmental variables in the RDA. The significance of the variables are tested by a Monte Carlo Permutation Test (Canoco; 999 permutations).

Marginal effects		Conditional effects		
Variable	λ_1	Variable	λ_A	p
diff Tsoil	0.38	diff Tsoil	0.38	0.001
diff Tair	0.34	Savanna	0.31	0.001
Tair start	0.33	Day	0.04	0.002
Day	0.32	Forest	0.02	0.001
Night	0.32	Tfaeces	0.02	0.008
Savanna	0.32	Tair end	0.01	0.066
Tsoil end	0.27	Tsoil start	0	0.508
Tsoil start	0.25	Tair start	0	0.960
Tair end	0.25			
Tfaeces	0.15			
Forest	0.10			
River	0.09			

Energetic constraints, ecological tolerance, physiological advantages and disadvantages

Forming dung balls (that weigh up to 80 times the beetle's body mass [Hanski and Cambefort 1991b]) and rolling them away rapidly is an energetically costly activity. Bartholomew and Heinrich (1978) found that the velocity of beetles increases with the body temperature, which in some species can be increased endothermically. Diurnal savanna species prefer sunny days when their body temperature is likely to be optimized by external heating. If their ability for endothermy is reduced, because it is rarely necessary in the savanna, they would avoid shady, cooler areas where they would be slower and competitively inferior to forest species. The RDA shows that temperature of faeces, soil and air are related to the abundance of telecoprids (which are diurnal). Diurnal soil and faeces temperatures are significantly lower in the gallery forest than in the open habitats (Table 3, $p < 0.05$). This could be the reason why rollers do not penetrate the gallery forest in a considerable number and do not reach the river valley, which would be a suitable habitat, at least for telecoprids and smaller paracoprids. The air temperature, however, does not differ significantly between savanna and gallery forest, but is significantly higher in the river valley. Why is the river valley not populated by thermophilous diurnal species?

The gallery forest is likely to be a flight barrier for savanna dung beetles that prefer sunny to shady places. Our knowledge about maximum height of flight and dispersal ability of Scarabaeidae is based on only a few anecdotal notes according to which the Scarabaeinae and Coprinae usually fly no > 5 m above the ground (Tippman 1959, Halffter and Matthews 1966: 89, Walter 1980, Davis 1993: 166). However, Aphodiinae are known to be mobile, sometimes migrating flyers (Roer 1968). Generally they forage between 0.5 and 3 m above ground (Schmidt 1935: 313), but if any ground-living dung beetles are captured in higher air layers, on trees, roofs or in migrating swarms, they always belong to the Aphodiinae (Felt and Chamberlain 1935, Glick 1939: 35, Williams et al. 1956, Roer 1968, Irmeler 1998). Exceptions to this rule are some highly specialized forest canopy Scarabaeidae of the tribes Onthophagini, Sisyphini and Canthonini (Walter 1984, Davis et al. 1997), a temperate *Onthophagus* species that was regularly found on the roof of a high building (Felt and Chamberlain 1935), and a single observation of the telecoprid *Pachylomera femoralis* Kirby flying over a forest (Walter 1980).

Virtually all Aphodiinae belong to the less competitive guild of endocoprids, but they have the highest potential for clearing barriers and settling in habitats which are generally inaccessible for members of competitively superior guilds. In our study, the barrier is the gallery forest, which is obviously insurmountable for

most paracoprids, telecoprids and their kleptoparasites. The crepuscular and nocturnal Aphodiinae (endocoprids), however, get to the river valley and dominate the coprocenoses there (Fig. 5 and Table 1). Moreover Aphodiinae seem to have a higher ecological potency to use different kinds of habitats and to cope with changeable microclimatic conditions than telecoprids or endocoprids, which seem to be more specialized and ecologically restricted. Our RDA (Fig. 7) shows that less increase/higher decrease of soil and air temperature during the experiment is correlated with a higher abundance of endocoprids and negatively correlated with the abundance of the telecoprids (and their kleptoparasites). The endocoprids seem to prefer a higher soil and air temperature at the start of the experiment, i.e. close to dusk, their main flight period, but they are at least tolerant of temperature decrease which is a general advantage for crepuscular or nocturnal species.

Escobar (1997) gives a further example for the occurrence of endocoprids in habitats that are less suitable for competitively superior groups. In Colombia he found that the portion of endocoprids were highest at forest edge and on pastures, i.e. in disturbed habitats not suitable for forest specialists. In a further study, he found a higher percentage of endocoprids in artificial pasture habitat where the autochthonous telecoprids and paracoprids do not settle (Escobar and Chacón de Ulloa 2000).

According to literature, the endocoprids (which form major part of the coprocenoses in temperate regions; Hanski 1991, Lumaret and Kirk 1991), "usually play an insignificant role" in Afrotropical coprocenoses (Cambebert 1984: 17, 1991: 161). As far as the assemblages of river valley and gallery forest are concerned, this statement has to be revised.

The bigger paracoprids which need a certain depth of the soil to make their burrows would take a risk when using the river valley because only a few places have a soil layer of > 10 cm. Since small Aphodiinae might be facultative kleptoparasites of paracoprids (Rougon and Rougon 1980), the latter may take a high risk to lose their offspring when they try to use a dung pat populated by hundreds or even more than a thousand endocoprids. The dung provided by the paracoprids for their offspring would be likely to be used by facultative kleptoparasites if they are numerous.

Conclusions

Significant differences in the guild structures among coprocenoses of different adjacent habitats indicate that habitat influences or even determines the guild structure of coprocenoses. species of competitively inferior guilds are to a certain extent separated spatially from species of competitively superior guilds and this may be one of the mechanisms that enables even the competitively

most inferior guild to persist sympatrically with the superior guilds. This is possibly driven by energetic constraints. The hierarchy of competitive superiority (dwellers < tunnellers < rollers) is combined with increasing energetic costs and, therefore, decreasing ecological tolerance. Rolling large dung masses away in a very short time most probably costs more energy per time than relatively slow tunnelling behaviour. The telecoprids are only superior competitors in a favourable environment, i.e. in the savanna during the day. When the temperature is lower, at night, the paracoprids use accessible habitats (savanna, gallery forest). The grassland of the river valley, which is isolated from the savanna by the gallery forest, is populated by the most inferior competitors but best flyers, the endocoprids – but only at night, when the telecoprids are not active in (accessible) open habitats. We suggest that the guild structure of coprocenoses in the forest savanna mosaic of the study area results from a trade-off between competitive superiority and energetic constraints. The low abundance in nocturnal forest coprocenoses is the only pattern that may be explained by an area effect.

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