

## The beetle fauna of hyaena latrines: coprocenoses consisting of necrophagous beetles (Coleoptera Trogidae Scarabaeidae)

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The scarab beetle fauna (Coleoptera Scarabaeoidea) on Spotted Hyaena, *Crocuta crocuta* (Erxleben 1777), scats was investigated to identify the feeding guilds of scarabs on an unusual dung substrate. During 19 months inspecting hyaena latrines and surrounding roads, 69 specimens of 8 species of Scarabaeoidea (Trogidae and Scarabaeidae) were collected from 200 hyaena faeces samples and 17 samples of regurgitated hairs. With increasing amount of hairs in the samples, attraction to hyaena faeces increased (from dry, white faeces to soft, brownish faeces to regurgitated hairs). Most of the scarab species that we found feed generally on carrion and omnivore/carnivore dung. Three species have not previously been found on carrion but are likely to be (facultative) necrophages. Further records of beetles from hyaena faeces indicate that almost all species that are attracted by this bait are at least facultatively necrophagous. The dung part of their diet consists mainly of omnivore or carnivore faeces as is usual for necro-coprophagous species.

KEY WORDS: dung beetle assemblage, hyaena faeces, necrophagy, coprophagy, Parc National de la Comoé, Côte d'Ivoire, Congo.

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## INTRODUCTION

Hyaenas defecate regularly in particular sites called latrines (BEARDER & RANDALL 1978). These sites are very conspicuous due to white scats. In the study area (Parc National de la Comoé in Côte d'Ivoire), scats together with regurgitations and urine are scattered over an area of 25 to 100 m<sup>2</sup> (variable between latrines and seasons). Hyaenas visit their latrines periodically, normally at least once a week as can be determined by spoors, scrapes, new scats and/or urination. Since Spotted Hyaenas live solitarily in the Comoé Park (KORB 2000), the latrines never have major accumulations of scats.

Faeces of hyaenas have an atypical dung appearance and odour. They are mostly white (SILLERO-ZUBIRI & GOTTELLI 1992: 171) and consist of "dry bone powder with a little hair of the prey" (KRUUK 1972: 66; see photograph in SKINNER & VAN AARDE 1981: 232). These calcium-rich, hard white lumps are less attractive to dung beetles (CAMBEFORT 1984: 247), therefore subject to much less intense decomposition processes and can remain visible for up to 14 months (BEARDER & RANDALL 1978: 35). About 15% of the faeces collected by SILLERO-ZUBIRI & GOTTELLI (1992) in Kenya were brown in colour. According to BEARDER & RANDALL (1978: 35) hyaenas produce such faeces after consumption of meat-rich food. These scats were soft in texture and were disintegrated by dung beetles within 3 days, particularly during the wet season (BEARDER & RANDALL 1978: 35, 45; KRUUK 1972: 66). KRUUK gave the species names of the "dung beetles" found on hyaena faeces: *Trox tuberosus* Klug 1855 (now in the genus *Omorgus* Erichson 1847, see SCHOLTZ 1986) and *T. luridus* Fabricius 1781. However, he did not mention the type of faeces.

WALTER (1978: 190ff, 202f, 208f) was the first and only researcher to bait dung beetles with hyaena faeces. In the former Zaïre, he collected 33 species with this bait in pitfall traps. No further information on the hyaena dung fauna has been published so far.

In Côte d'Ivoire, one of us (J. Korb) studied the population of Spotted Hyaenas, *Crocuta crocuta* (Erxleben 1777) (KORB 2000). During regular inspections of latrines and from faeces collected elsewhere, all beetles were extracted from hyaena dung and regurgitations. The species were identified to determine whether Spotted Hyaena scats, which have both dung and carrion characteristics, attract coprophagous or necrophagous species.

## MATERIAL AND METHODS

We conducted our study in the Parc National de la Comoé in the north-eastern Ivory Coast (= Côte d'Ivoire, West Africa) around the research camp of the University of Würzburg (Lola-Camp). The study area is situated at the border between the Guinean and Subsdan savanna attributed by POREMBSKI (1991) to the former and by POILECOT (1991), amongst others, to the latter. The latrines were located in the savanna around 3°47'-50'W and 8°44'-50'N (KORB 2000).

J. Korb inspected the latrines once a week from February 1997 to August 1998. Beetles were collected by hand from hyaena faeces or regurgitated hairs from 29 March 1997 to 13 August 1998. They are deposited in The Natural History Museum, London.

The following substrates were studied:

(i) Hard, white faeces. Calcium-rich scats due to meals that consist of a rather high proportion of bones that hyaenas can crush with their strong jaws and which they can partially digest. These scats are sausage-shaped (diameter: 2-4 cm, length: 5-17 cm) and of a dry, rather porous consistency, but still contain many hairs.

(ii) Soft, brownish faeces. The soft faeces of the hyaenas of the Comoé Park contain a great amount of fur. Since their odour is not obviously stronger than that of the white faeces, it is unlikely that they result from a meat-rich diet. More likely it is an indicator of a bone-poor diet. Meat-rich faeces always have a strong odour due to a high proportion of metabolic products of meat digestion (e.g., brown hyaena faeces in South Africa, BEARDER & RANDALL 1978: 35). The soft faeces were about 1 cm high and 5-10 cm in diameter.

(iii) Regurgitated hairs. Clumps of hair that are held together with saliva.

## RESULTS

Relatively few scats were used by scarabs. J. Korb collected 183 faeces samples and 17 regurgitations. Thirty-five of the faeces samples were old and probably unattractive for Scarabaeoidea, 5 were from young presumably suckling animals. Both types of faeces did not contain any scarab beetles. Of the 160 potentially attractive samples, only 13 (8.1%) were used by Scarabaeoidea. Of the 93 dry, white faeces samples, 4.3% (4) were visited by beetles, while 18.0% (9) and 23.5% (4) of the 50 soft samples and 17 regurgitations, respectively, attracted beetles. Thus attraction differed significantly between the different substrata ( $n = 160$ ,  $\chi^2 = 9.76$ ,  $P = 0.008$ ) and increased from dry, white faeces to soft faeces to regurgitations (Spearman rank correlation:  $r = 0.247$ ,  $P = 0.002$ ).

In comparison with other dung or carrion types, few Scarabaeoidea species were found on hyaena faeces and regurgitated hairs. We found two species (14 specimens) on white faeces, five species (57 specimens) on soft faeces and five species (12 specimens) on regurgitations (Table 1). All but three species feed regu-

Table 1.

Results of beetle collecting from hyaena faeces and regurgitations during the study period 29 March 1997-13 August 1998 in the Parc National de la Comoé, Côte d'Ivoire.

Species	Substratum			Total
	White faeces	Brown faeces	Regurgitated hairs	
<i>Omorgus melancholicus</i>	7 ♂♂, 5 ♀♀	14 ♂♂, 15 ♀♀	1 ♀	42
<i>Omorgus gemmatus</i>	—	5 ♂♂	1 ♂	6
<i>Omorgus guttalis</i>	—	2 ♂♂, 2 ♀♀	—	4
<i>Anachalcos suturalis</i>	—	4 ♀♀	1 ♂, 5 ♀♀	10
<i>Onthophagus antennalis</i>	—	—	1 ♀	1
<i>Onthophagus flexicornis</i>	—	—	2 ♂♂	2
<i>Onthophagus rufonotatus</i>	—	3 ♀♀	—	3
<i>Onthophagus rufostillans</i>	1 ♂	—	—	1
Total	13	45	11	69

larly on carrion and omnivorous dung (Table 2). One is only known from omnivorous and carnivorous dung. The feeding habits of the two remaining species are unknown. The eudominant species, *Omorgus melancholicus* (Fahraeus 1857), is primarily necrophagous.

Table 2.

Characterization of the beetle species collected at hyaena faeces in the Parc National de la Comoé, Côte d'Ivoire.

Species	Feeding preferences	Distribution
<i>Omorgus melancholicus</i> (Fahraeus 1857) (Trogidae)	consistently necrophagous (BRAACK 1986); carrion and human faeces (ENDRÖDY-YOUNGA 1982); carrion, faeces of lion, human and rarely of buffalo, not on hyaena faeces (WALTER 1978)	most of Afrotropics, moist savanna regions (SCHOLTZ 1980)
<i>Omorgus guttalis</i> (Haaf 1954) (Trogidae)	unknown	Senegal, Mali, Burkina Faso, Ghana and Nigeria (HAAF 1954, SCHOLTZ 1980). First record for Côte d'Ivoire
<i>Omorgus gemmatus</i> (Olivier 1789) (Trogidae)	unknown; recorded from eggs of the migratory locust (RISBEC 1946)*	Sub-Saharan savanna belt, also in Saudi Arabia and Egypt, arid areas (HAAF 1954, SCHOLTZ 1980). First record for Côte d'Ivoire
<i>Anachalcos suturalis</i> Janssens 1938 (Scarabaeidae)	human and other omnivore faeces, carrion	Nigeria, Ghana, Côte d'Ivoire, savanna biomes (CAMBEFORT 1984)
<i>Onthophagus antennalis</i> Frey 1961 (Scarabaeidae)	human faeces, "divers petits excréments", presumably of carnivores	DR Congo, Côte d'Ivoire (CAMBEFORT 1984)
<i>Onthophagus flexicornis</i> d'Orbigny 1902 (Scarabaeidae)	different faeces, carrion	West African savanna biomes (CAMBEFORT 1984)
<i>Onthophagus rufonotatus</i> d'Orbigny 1902 (Scarabaeidae)	omnivorous and herbivorous dung, carrion, mushrooms	widely distributed in the Afrotropics (CAMBEFORT 1984)
<i>Onthophagus rufostillans</i> d'Orbigny 1907 (Scarabaeidae)	human faeces, carrion	northern DR Congo, Togo, Côte d'Ivoire (CAMBEFORT 1984)

\* Because some further species of the *O. gemmatus*-group occurring in Senegal have been described since, RISBEC's record needs confirmation.

## DISCUSSION

*The coprocenoses of hyaena dung, a substrate with dung and carrion characteristics*

Most of the species that we found on hyaena faeces are necrophagous. These data corroborate WALTER'S (1978) results from trapping experiments in the former Zaïre. He did not find strong attraction to white hyaena faeces of any dung beetle species, but only a medium to low effect, which means a maximum of 40% of the traps were attractive (WALTER 1978: 190ff; see Table 3). The odour of white hyaena faeces is nearly imperceptible to humans and is unattractive for dung beetles when faeces are exposed on the bottom of a pitfall trap (WALTER 1974). Overall, 52% of the 75 traps did not attract a single beetle within 24 hr. The 38 successful traps attracted 157 specimens of Scarabaeidae.

WALTER'S trapping results (rearranged in Table 3) show the trophic preferences of the beetles, attracted by hyaena faeces. Since he used traps, he collected all beetles that approached the faeces, not only those beetles which actually used the faeces as a resource. Generally a higher number of specimens can be captured with traps than by bait that is exposed on the ground (LOBO et al. 1988) but distinguishing between tourists and actual users of the resource is impossible.

All but one species he trapped are at least partially necrophagous; the tendency to necrophagy is slightly stronger in the beetles which were more often attracted to hyaena faeces. Only one purely coprophagous species was trapped, which prefers omnivorous dung (chimpanzee). Most of the species prefer a diet of omnivorous dung combined with carrion. Only the group of beetles in which low attraction to hyaena faeces was observed contained a higher number of species that accept herbivorous dung. Walter's results show the tendency that a higher acceptance of hyaena faeces is positively correlated with necrophagy and negatively correlated with the preference for herbivorous dung. In dung beetles, necrophagy is a common nutritional habit all over the world (WALTER 1983, VEIGA 1985). However, strict necrophagy is rare (WALTER 1983, CAMBEFORT 1984: 255). Carrion feeding species often accept carnivore or even omnivore dung (DOUBE 1987).

*Feeding ecology of Trogidae, the most frequent beetles on hyaena dung*

The "dung beetles" collected by KRUK (1972) on hyaena faeces were identified as *Omorgus tuberosus* Klug and *Trox luridus* Fabricius (Trogidae). However, Trogidae are not dung beetles. Trogidae, the most frequent beetles in our samples, are generally necrophagous and feed regularly on keratinous matter (SCHOLTZ 1986). Four species of *Trox* Fabricius 1775 have been recorded to be predacious to locust eggs (ROFFEY 1958) and one, *Omorgus suberosus* (Fabricius 1775), feeds on turtle and land iguana eggs on Galápagos and México (ALLGÖWER 1980, ROSANO-HERNÁNDEZ & DELOYA 2002). Several species of the genus *Trox* have been collected on carnivore and omnivore dung (cat, dog, fox, lion, racoon, opossum, baboon, human, swine and bats; GERHARDT 1887, FINCHER et al. 1970, WALTER 1978: 208, SCHOLTZ 1980, LUMARET 1983). Trogidae are rarely found on herbivore dung. Only a few specimens have so far been found on horse, cow and buffalo dung (FINCHER et al. 1970, WALTER 1978: 208, MARTÍN-PIERA & LOBO 1996). In summary, Trogidae show the general feeding pattern of necrophagous Scarabaeoidea accepting carnivore and omnivore rather than herbivore dung.

Table 3.

Feeding preferences and attraction of Scarabaeidae species to hyaena faeces in Zaire (Plateau Bateke) after WALTER (1978).

Overall nutritional preferences (number of species in study area in brackets)	Low attraction of hyaena faeces species in < 10% of the traps	Medium attraction of hyaena faeces species in 10-40% of the traps
C (9)	0	1
Cn (35)	14	2
CN (13)	3	6
cN (7)	2	3
N (1)	0	0
Nutritional preferences according to most attractive bait i.e. species in > 40% of the traps (number of species in study area in brackets)	Low attraction of hyaena faeces species in < 10% of the traps	Medium attraction of hyaena faeces species in 10-40% of the traps
hv/ov (13)	7	3
ov (32)	9	1
ov/N (12)	1	6
hv/ov/N (3)	0	1
N (5)	2	1

C: coprophagous. Cn: copro-necrophagous with tendency to coprophagy. CN: copro-necrophagous without clear preferences; cN: necro-coprophagous with tendency to necrophagy; N: necrophagous. No coprophagous species was found only on hyaena faeces; hv: herbivorous dung; ov: omnivorous dung (including carnivorous dung); N: carrion. There was no specialist for herbivore dung.

Low attraction to *Pachylomerus femoralis* (Kirby 1828), *Scarabaeus kwiluensis* Janssens 1940, *Gymnopleurus jacksoni* Waterhouse 1890, *Liatongus interruptus* (Quedenfeldt 1884), *Catharsius biconifer* Felsche 1907, *Metacatharsius bateke* Walter 1976, *Copris cassius angolensis* Ferreira 1962, *C. inhalatus* Quedenfeldt 1884, *Caccobius curvicornis* Walter & Cambefort 1977, *Caccobius histrio* Balthasar 1967, *Onthophagus caelator* Balthasar 1967, *O. crantor* Balthasar 1967, *O. impressicollis* var. *circuitus* d'Orbigny 1902, *O. lefiniensis* Balthasar 1967, *O. xanthochlorus* Walter & Cambefort 1977, *O. indutus* d'Orbigny 1902, *O. umbratus* d'Orbigny 1902, *Proagoderus monochromus* (d'Orbigny 1913), *P. speculatus* (d'Orbigny 1908).

Medium attraction to *Sisyphus crispatus* Gory 1833, *Catharsius luluensis* Ferreira 1960, *Onthophagus altidorsis* d'Orbigny 1905, *O. calchas* Balthasar 1967, *O. duvivieri* d'Orbigny 1904, *O. reticulatus* d'Orbigny 1902, *O. sylvestris* Walter & Cambefort 1977, *O. tuzetae* Walter & Cambefort 1977, *O. varieganosus* d'Orbigny 1905, *Proagoderus opulentus* (d'Orbigny 1902), *P. speculicollis* (Quedenfeldt 1884), *Anachalcos cupreus* (Fabricius 1775) (all Scarabaeidae).

Additionally, WALTER (1978: 202) trapped two rare species with hyaena faeces: *Neoisophus spinipes* (Thunberg 1818) and *Onthophagus brazzavillianus* Balthasar 1974.

A significantly higher proportion of the brownish, soft faeces and regurgitation samples attracted scarab beetles than did dry white faeces. Both of these attractive substrata are moist and rich in keratinous material (the primary resource for *Omorgus* species). Whether it is one of these factors or a slightly different odour that caused the higher attractivity cannot be concluded here. The higher

attractivity of moist substratum to *Omorgus* (10.0% / 11.8%) is, however, not significantly different from the attractivity of dry faeces (4.3%) (extension of Fisher test).

### *Concluding remarks*

Strict trophic specialisation is relatively rare in Scarabaeidae and Trogidae. Many species accept carrion as well as dung. Particularly if the substrata are similar as are rotting animals and digested animals, the same species may use them. This is the case with the necro-coprophagous Onthophagini that we found during this study. If there are some keratinous materials in the dung, such as fur, necrophagous keratin feeding Trogidae may use them as they do in hair-rich hyaena faeces or regurgitated hairs. Fur and bones give hyaena dung a character of something inbetween dung and carrion and make it attractive for primarily necrophagous species.

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