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DIURNAL AND NOCTURNAL FLIGHT ACTIVITY OF SCARABAEINE COPROPHAGES IN TROPICAL AFRICA

Activités de vol diurnes et nocturnes des Scarabéinés coprophages de l'Afrique tropicale.

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RESUME

Le dénombrement des scarabéinés coprophages capturés heure par heure à l'aide d'un piège a permis une détermination précise du moment de la journée pendant lequel a lieu les différentes activités de vol dans les cas de 87 espèces de savane et de forêt présentes sur le plateau Bateke au Zaïre (72 Scarabaeidae, 13 Aphodiidae, 2 Trogidae). Pour certaines de ces espèces ainsi que pour beaucoup d'autres, des observations personnelles ont été effectuées au Gabon et dans la République Populaire du Congo. Les données récente de CAMBEFORT relatives à la Côte d'Ivoire ont également été prises en considération. De ce fait, le nombre total d'espèces étudiées dépasse 400.

Tous les Aphodiidae et Trogidae capturés sont nocturnes. En ce qui concerne les Scarabaeidae, une analyse de détail a permis de distinguer des caractéristiques communes au niveau de neuf tribus, de certains genres et avec plus de précisions, des espèces du plateau Bateke.

ABSTRACT

The yield hour by hour from coprophages pitfall traps have permitted a precise determination of the hours of flight activity concerning 87 savanna or forest species present on the Bateke Plateau in Zaïre (72 Scarabaeidae, 13 Aphodiidae, 2 Trogidae). For certain of these species, as well as for others, data also has been collected in Gabon and in the Popular Republic of Congo. We have also taken in consideration the recent data from CAMBEFORT concerning the Ivory Coast. Thus, this study concerns more than 400 species.

All of the Aphodiidae and Trogidae found are nocturnal. As for the Scarabaeidae, a detailed analysis has permitted to discern common caracteristics at the level of nine tribes. at the level of some genus. or with greater precision, at the level of Bateke Plateau species.

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INTRODUCTION

Until recently, there was little information about flying out of *Scarabaeidae*[1], *Aphodiidae*[1] and *Trogidae* in tropical Africa. After many authors had quoted their captures with light-traps, the nocturnal character of the flight could be established for some species of them; among other authors let us quote BOUCOMONT (1935). HAAF (1959), FREY (1961), FERREIRA (1962), BALTHASAR (1967), ENDRODI (1967)[2], CAMBEFORT (1972), KRIKKEN (1974). But these data too scattered through litterature are essentially limited to the knowledge of an autecological characteristic of the species, which therefore gives them only a relative value. The species that were quoted as explicitly diurnal are also very few, with sometimes - consequence of a hasty generalization - wrong assertions such as the one which, for example, classified all the ball-rolling beetles as being diurnal (JANSSENS, 1940).

Recent works, specially those directed to ecology and biology of these afro-tropical scarabaeines, bought more numerous and above all more precise data about the hours of flight activity and about the ecological factors apt to influence this activity : they are, among others, the works of TRIBE (1976) in Southern Africa, WALTER (1978) in Zaïre, and CAMBEFORT (1982, 1984) in Ivory Coast. If CAMBEFORT and WALTER attached themselves to set out the place occupied respectively by the diurnal and nocturnal populations among the various forest and savannah faunas studied, TRIBE, as for him, analysed the influence of temperature on the flight activity of some diurnal species.

The whole lot of these data concerning many hundreds of species, permit henceforth to set out some major principles at the level of the genus, indeed at the level of tribes, and savannah and forest faunas as well. It is then in order to put these principles into evidence that we intend to synthesize here our personal observations in Zaïre, in the People's Republic of Congo and in Gabon, observations that will be usefully completed by the numerous and important data of CAMBEFORT, and accessorily by those of TRIBE.

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(1) sensu BALTHASAR (1963).

(2) To be exploited for the present topic, these two last works must be completed refering to BALOGH et al. (1965).

ORIGIN OF THE MAIN DATA

1. The example of forest and savannah faunas of the Bateke Plateau in Zaîre

Covered with a mosaic of savannahs and secondary forests, the Bateke Plateau in Zaîre presents as a whole a varied scarabaeine fauna, since we have recorded 112 species of *Scarabaeidae* distributed between 9 tribes (WALTER & CAMBEFORT, 1980), 31 species of *Aphodiidae* and 2 species of *Trogidae* (WALTER, 1981).

1.1. Methods

To study in particular the flight activity, two trapping operations were executed near Menkao (15° 42' 8" E, 4° 11' 16" S) :

- the first one during 48 hours consecutively (10.1.1976, 3 p.m.[1] to 12.1.1976, 3 p.m.) in contact of a shrubby savannah and a secondary forest. In each of these two vegetation formations four pitfall traps were set, with thirty meters distance between them. Two kinds of baits were put alternately in the traps, baboon excrement and rotten fish, for past experiments showed that one of those two baits at least attracted most of the common species of the Plateau. Every hour all the traps were changed and immediately replaced by new baits of the same sort. The insects caught in the traps were sorted out at the bivouac.
- the second one during 24 consecutive hours (11.3.1976, 9 a.m. to 12.3.1976, 9 a.m.), in grassy savannah, with six traps and the same experimental procedure.

During the two experiments the variation of some climatic factors (temperature, hydrometry, luminosity, wind speed) were noticed (WALTER, 1978, appendix).

1.2. Results

The tables I, II, III (*Scarabaeidae*) and IV (*Aphodiidae* and *Trogidae*) present a synthesis of the observations made during the two operations[2]. In this synthesis were also enclosed some complementary observations made on diurnal species from 1973 to 1977 in the same region, and also in the People's Republic of Congo. For all the three families then, we have been able to determine the hours of flight activity for

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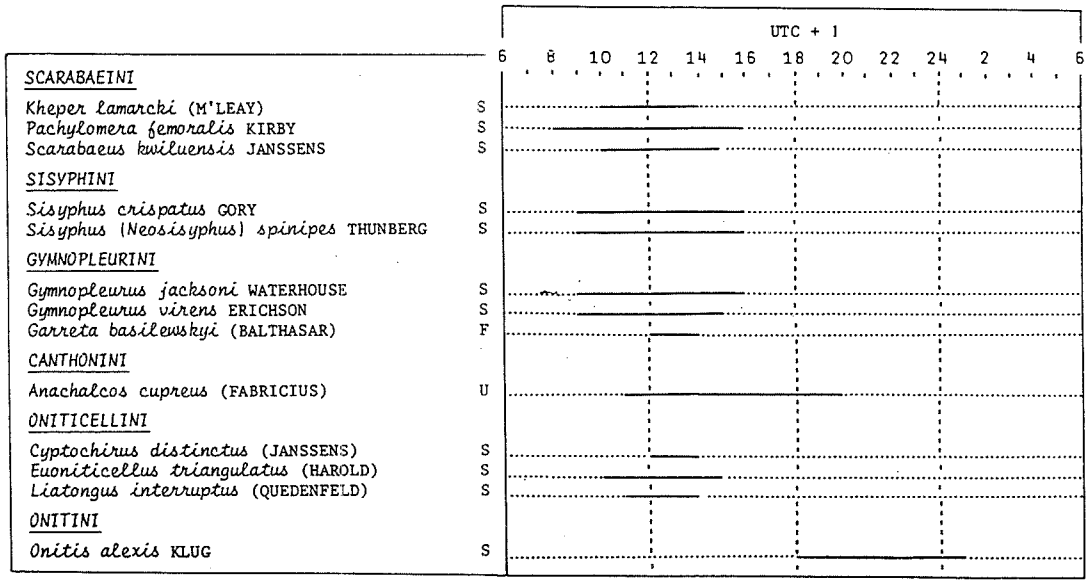
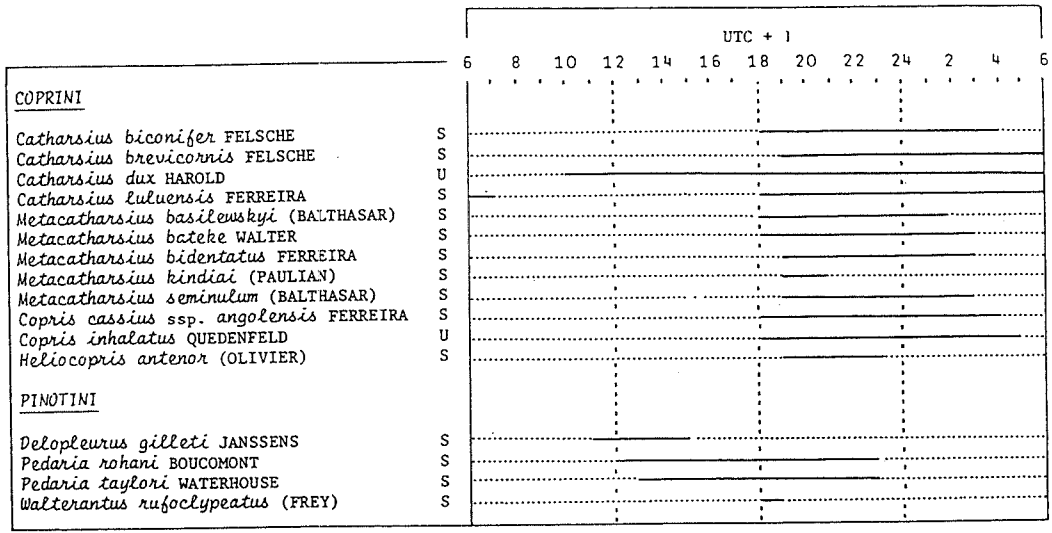
(1) Local time = UTC + 1.

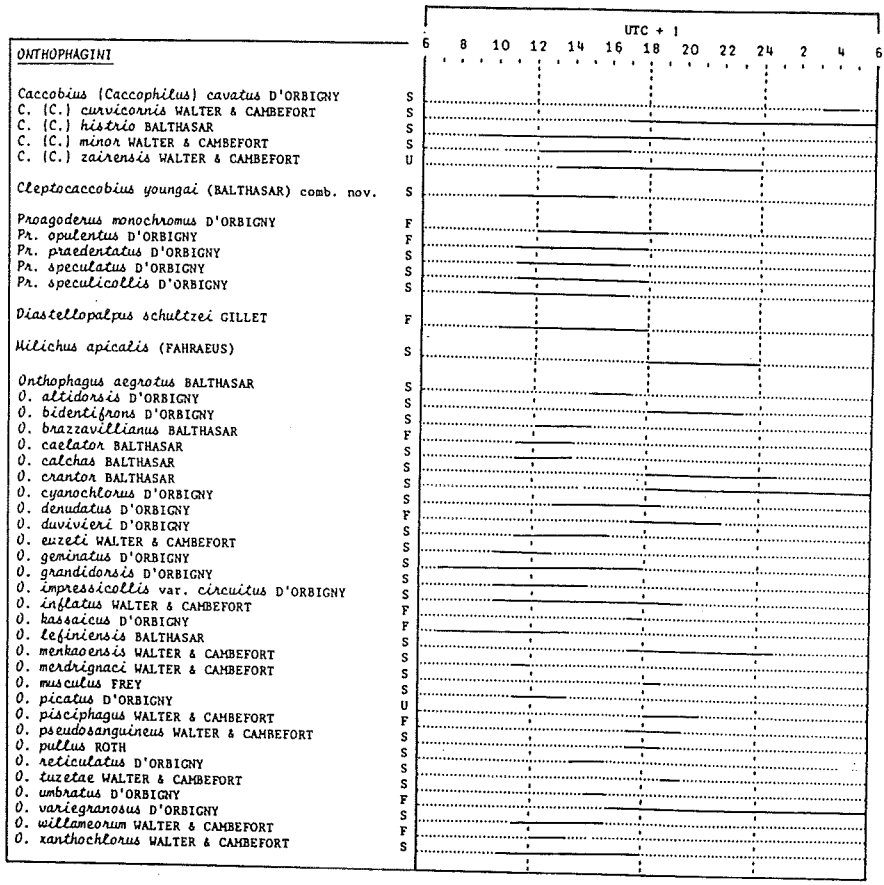
(2) For more details concerning the captures hour by hour, see WALTER (1978, appendix)



Tab. I : Flying time of some *Scarabaeidae* occuring on the zaïrean Bateke Plateau : *Scarabaeini*, *Sisyphini*, *Gymnopleurini*, *Canthonini*, *Oniticellini* and *Onitini*. S = savannah species; F = forest species, U = ubiquitous species.

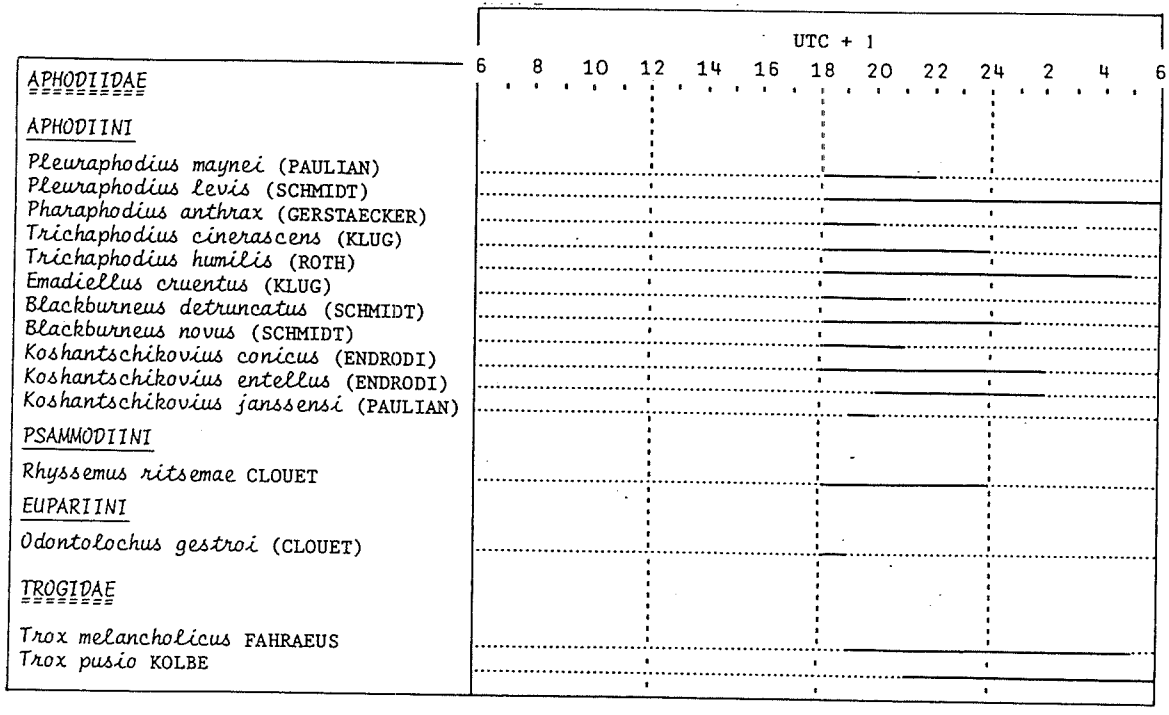


Tab. II : Flying time of some *Scarabaeidae* occuring on the zaïrean Bateke Plateau : *Scarabaeini*, *Sisyphini*, *Gymnopleurini*, *Canthonini*, *Oniticellini*, *Onitini*, *Coprini* and *Pinotini*. S = savannah species; U = ubiquitous species ; F = forest species.



Tab. III : Flying time of some *Scarabaeidae* occuring on the zaïrean Bateke Plateau : *Scarabaeini*, *Sisyphini*, *Gymnopleurini*, *Canthonini*, *Oniticellini*, *Onitini*, *Coprini*, *Pinotini* and *Onthophagini*. S = savannah species; F = forest species; U = ubiquitous species.

87 species. For the *Scarabaeidae* only, the table V condensates these results indicating for each tribe the number of diurnal, nocturnal or indifferent species, in savannah and in forest.



Tab. IV : Flying time of some *Aphodiidae* and *Trogidae* occuring on the zaïrean Bateke Plateau (all species are savannah species).

	SAVANNAH SPECIES			FOREST SPECIES			UBIQUITOUS SPECIES		
	D	N	D/N	D	N	D/N	D	N	D/N
Scarabaeini	3	-	-	-	-	-	-	-	-
Sisyphini	2	-	-	-	-	-	-	-	-
Gymnopleurini	2	-	-	1	-	-	-	-	-
Canthonini	-	-	-	-	-	-	-	-	1
Oniticellini	3	-	-	-	-	-	-	-	-
Onitini	-	1	-	-	-	-	-	-	-
Coprini	-	10	-	-	-	-	-	1	1
Pinotini	1	1	2	-	-	-	-	-	-
Onthophagini	19	8	4	5	4	1	-	1	1
Total	30	20	6	6	4	1	0	2	3

Tab. V : Numbers of diurnal and nocturnal species, in the different vegetation formations on the zaïrean Bateke Plateau (for 72 *Scarabaeidae*). D = diurnal species; N = nocturnal species, D/N = indifferent species.

2. Other data

2.1. *Gabon*

Diurnal traps (set from 7:30 a.m. to 17:30 p.m.) and crepuscular and nocturnal traps (set from 17:30 p.m. to 7:30 a.m.) permitted to define the diurnal or nocturnal character of flight for 57 species of forest *Scarabaeidae* (Tab. VI), and 2 species of *Trogidae* (1981-1983, regions of Bifoun and Makokou).

	D	N	D/N
Sisyphini	2	-	1
Gymnopleurini	1	-	-
Oniticellini	3	-	-
Onitini	-	3	-
Coprini	-	8	-
Pinotini	-	1	-
Onthophagini	15	11	12
Total	21	23	13

Tab. VI : Numbers of diurnal and nocturnal species for 57 forest species in Gabon. D, N, D/N : see Tab. V.

2.2. *Ivory Coast*

For all the stations studied in this country, CAMBEFORT (1984) precised the diurnal or nocturnal character for 283 *Scarabaeidae* species, data we summarized in table VII.

	FOREST		SAVANNAH	
	D	N	D	N
Scarabaeini	-	-	3	1
Sisyphini	9	-	11	-
Gymnopleurini	1	1	7	1
Canthonini	1	1	1	4
Oniticellini	9	-	18	-
Onitini	-	6	-	13
Coprini	-	12	-	23
Pinotini	-	-	2	9
Onthophagini	31	36	48	45
Total	51	56	90	96

Tab. VII : Numbers of diurnal and nocturnal *Scarabaeidae* species for the whole of several stations in Ivory Coast (after CAMBEFORT's data, 1984).

2.3. *Southern Africa*

In the Mkuzi Game Reserve, TRIBE (1976) studied the hours of flight activity for about ten diurnal or nocturnal *Scarabaeidae* species(1), in relation with the variations of temperature.

DISCUSSION

1. *Scarabaeidae*

1.1. *Analysis at the level of tribes and their main genus*

About a few decades ago only the non-ball-rolling species were still thought to have a nocturnal activity, the ball-rolling ones (*Scarabaeini*, *Gymnopleurini*, *Sisyphini* above all) being considered as very heliophilous for most of them. The review of the main genus, tribe after tribe, permits to push aside this conception once for all.

- *Scarabaeini*.

After FERREIRA (1968-1969) who considered the genus *Scarabaeus* as a diurnal one, we had extended this character to all the tribe (WALTER, 1978). Such a generalization can non longer be kept, because at least two exceptions are known from now on. The first exception is that represented by *Scarabaeus goryi* (CASTELNAU) which is nocturnal (CAMBEFORT,

(1) And some undetermined Histeridae.

1984); if ourself we trapped in Zaïre two individuals in the day (between 10 a.m. and 1 p.m.), this can perhaps be explained by the fact that it is about a relict population in the dition, with an individual behaviour likely to be disturbed, or by the fact that it could be about an "apportunist" species in the meaning of CAMBEFORT (*loc. cit.*). The other exeption, quoted by TRIBE (1976), is that of *Scarabaeus zambesianus* PERINGUEY that flies at twilight and at dawn; this author also signals that *Kheper nigroaeneus* (BOHEMAN) besides being diurnal is met nearly in the morning and late in the afternoon. This species is not therefore so heliophilous as most of afro-tropical *Scarabaeini*.

- *Sisyphini*.

All *Sisyphus* and *Neosisyphus* are diurnal. Yet, as for *Sisyphus arboreus* WALTER, a species that lives in the canopy (WALTER, 1983), some individuals fly at twilight or at night.

- *Gymnopleurini*.

Only a species of this tribe is known as nocturnal, *Gymnopleurus profanus* (FABRICIUS), that flies at twilight and at dawn (CAMBEFORT, 1984), an activity that is then of the type of *Scarabaeus zambesianus* PERINGUEY mentioned above.

- *Canthonini*.

The *Anachalcos* appear to be rather nocturnal insects, but with variants from a species to another. If *A. aurescens* BATES is strictly nocturnal (Ivory Coast, Gabon), *A. cupreus* (FABRICIUS) seems indifferently diurnal or nocturnal (Ivory Coast, Zaïre), a particularity that must probably be related to the fact that the latter species can be seen in savannah and in forest as well (WALTER, 1977, 1978; CAMBEFORT, 1984). In Southern Africa *A. convexus* (BOHEMAN) is crepuscular (TRIBE, 1976), but CAMBEFORT (1984) notices that in Ivory Coast this species can also be seen in the day because of an "opportunist" behaviour. Finally, *A. suturalis* JANSSENS is presented by the latter author as a nocturnal species, but which is "*surtout active au petit matin, parfois jusque vers 8 H*".

As to *Odontoloma*, if we refer to the example of *O. relicta* CAMBEFORT in Ivory Coast (CAMBEFORT, *loc. cit.*) they might be day-flying insects.

- *Coprini*.

This tribe appears very homogenous as far as the ethological character studied here is concerned: for the genus *Catharsius*, *Metacatharsius*, *Copris*, *Heliocopris* and *Pseudopedaria*, the many species whose hours of flight activity were able to determine are all nocturnal.

Nevertheless, *Catharsius dux* HAROLD, an ubiquitous species of the Bateke Plateau in Zaïre shows itself in the day in forest biotopes.

- *Pinotini*.

Differently from *Coprini* that they are close to though, *Pinotini* show no general tendency. Are diurnal the *Copthorina* (TRIBE, 1976; CAMBEFORT, 1984) and *Delopleurus gilleti* JANSSENS (WALTER, 1978; CAMBEFORT, *loc. cit.*). On the contrary the *Pseudosaproecius* (CAMBEFORT, 1982) and *Walterantus rufoclypeatus* (FREY) (WALTER, 1978) are nocturnal. As for the *Pedaria*, most of species are nocturnal but a few of them can be indifferently diurnal or nocturnal such as *P. taylori* WATERHOUSE and *P. rohani* BOUCOMONT.

- *Onitini*.

All of them are night flying insects, for no exception was remarked.

- *Oniticellini*.

All species are diurnal.

- *Onthophagini*.

At the level of the genus of this important tribe, the character is quite notable for *Amietina*, *Cleptocaccobius*, *Phalops* and *Proagoderus* that are diurnal, and for *Milichus*, *Mimonthophagus* and *Strandius* that are nocturnal.

For the *Caccobius*, there seems to be as many diurnal species as nocturnal species, but some of them (*C. histrio* BALTHASAR, *C. zaïrensis* WALTER & CAMBEFORT) are indifferent.

The *Diastellopalpus* are also diurnal or nocturnal depending on the species, with also somme indifferent species such as *D. tridens* (FABRICIUS) (CAMBEFORT, 1984) or *D. conradti* D'ORBIGNY.

Finally, in the large group of *Onthophagus*, there seems to be sensibly the same numbers of diurnal and nocturnal species, to which must

be added not a negligible quantity of indifferent species at various degrees.

1.2. Flight activity : comparison between savannah and forest

HALFFTER & MATTHEWS (1966), from observations made in Mexico mainly, asserted that in tropical regions the diurnal species are more numerous in open biomes, while in the forests nocturnal species are dominant. These authors thereafter deduced that life in tropical evergreen forest was at the origin an essentially nocturnal one.

But the data related to intertropical Africa do not corroborate these assertions, particularly, in forest areas, as the following examples can show it.

In the forest of Makokou (Gabon), for 45 species whose the character was precised, we set out 19 diurnal species (42 %), 17 nocturnal species (38 %) and 9 indifferent species (20 %). In Zaïre, in the secondary forest of Bateke Plateau, we observed 6 diurnal species, 4 nocturnal and one indifferent.

In Ivory Coast, the date of CAMBEFORT (1984) permit us to distinguish :

- in the forest of Lamto (without taking in account savannah species that can enter the forest) : 23 diurnal species (72 %) and 9 nocturnal (28 %),
- in the forest of Sipilou : 21 diurnal (64 %) and 12 nocturnal (36 %),
- in the forest of Taï : 33 diurnal (45 %) and 41 nocturnal (55 %); and for the all forest stations studied in this country : 56 nocturnal species (52 %) and 51 diurnal species (48 %).

For the forest biotopes, we can then see that it is only in Taï that the rule of HALFFTER & MATTHEWS is respected; for the other four stations mentioned, which are geographically quite disjoined, and for the whole Ivory Coast, we observe either a highter number of diurnal species (and sometimes more significantly as in Lamto) or, for the diurnal and nocturnal species, numbers that are of the same order.

It is also impossible to generalize for savannah areas. If quite 60 % of diurnal species[1] can be seen on the Bateke Plateau in Zaïre, this percentage decreases, according to the data of CAMBEFORT (1984),

(1) Putting aside the indifferent species.

until it becomes non-significant for three stations in the Ivory Coast : 57 % for Abouamékro, 53 % for Lamto, 51 % for Sipilou. In Ouango Fitini, another station in the Ivory Coast where rainfall is lower, the proportion is even reverse with 57 % of nocturnal species. And among the 186 savannah species recorded by this author for all the stations, there are 96 nocturnal and 90 diurnal species(1).

More nocturnal species in forest areas, more diurnal species in open areas : this rule by HALFFTER & MATTHEWS, drawn from observations of neo-tropical scarab faunas relatively poorer than afro-tropical faunas, cannot be applied to Africa. Nevertheless, this does not exclude as much the hypothesis by these authors according to which life in the forest would be nocturnal at the origin, an hypothesis which remains valid.

We can also remark that the ubiquity (that is to say the particularity for a species to live either in savannah or in forest) often goes with flight activity which is indifferently diurnal or nocturnal. Thus, among five ubiquitous species on the Bateke Plateau in Zaïre, three of them have a diurnal and nocturnal flight but with variations linked to the sort of vegetation occupied (Tab. VIII); for all the cases yet, the ubiquity always happens at night and it is then possible that originally nocturnal habits lead this ubiquity.

	DIURNAL IN FOREST	DIURNAL IN SAVANNAH	NOCTURNAL IN FOREST	NOCTURNAL IN SAVANNAH
Anachalcos cupreus (FABRICIUS)	+	+	+	+
Catharsius dux HAROLD	+	-	+	+
Copris inhalatus QUEDENFELD	-	-	+	+
Caccobius zairensis WALTER & CAMBEFORT	-	+	+	+
Onthophagus picatus D'ORBIGNY	-	-	+	+

Tab. VIII : Flying activity of 5 ubiquitous species occuring on the zaïrean Bateke Plateau.

1.3. *Nocturnal flight*

Including the crepuscular ones, the nocturnal species can be put in three groups :

(1) About ten species also met in the forest are included.

- a group of species that fly during the first part of the night, with the first soaring possibly as soon as at twilight. This group is composed of a majority of species,
- a group of species that fly all the night till dawn. It is possible to think that we are in presence of species with pronounced vagility, a particularity that implies many repeated taking flight or even a minimum time of activity in flight during the same night, or species whose trophic needs are well defined, which makes the searching for a food source longer. Anyway, compared to the previous group, these species present a larger ecological valence as far as the factors of temperature and hydrometry are concerned : in fact, between 4 or 5 a.m. those two factors reach the limits of their values for the area considered, a minimal value for the temperature and a maximum value for the hygrometry. A lot of *Coprini* are included in this category,
- some rare species corresponding to the "*dawn and dusk species*" of TRIBE (1976), this author quoting *Scarabaeus zambesianus* PERINGUEY, and CAMBEFORT (1984) *Gymnopleurus profanus* (FABRICIUS). As to us, we did not disclose any species corresponding to this pattern on the Bateke Plateau in Zaïre. The factor of light quantity intervening less in the forest than in the savannah, it is possible that the species of this group are met only in open areas.

1.4. Diurnal flight

Considered as a whole, the observations of TRIBE (1976) on about ten species of the Mkuzi Game Reserve differ radically from those we made ourself on the Bateke Plateau and whose main results had been given on tables I, II and III (though the activity peaks are not mentioned on them).

Thus, in the dition of TRIBE, it can be observed, even in overcast weather, an intensive flight activity between 6 and 11 a.m., followed by an important decrease of this activity during the hottest hours of the day (between 11 a.m. and 1 p.m.), with possibly a recrudescence of activity in the afternoon. So that we can distinguish two categories of species :

- species whose flight activity is maximum in the morning, with from 10 or 11 a.m. a progressive decrease until 4-6 p.m.; *Phalops flavocinctus* (KLUG) for example,
- more numerous species showing two periods of important activity, one in the morning, the other, more diminished, in the afternoon, periods

which are separated by a clear decrease toward 11 a.m.-1 p.m. : *Gymnopleurus virens* ERICHSON, *Garreta nitens* (OLIVIER).

In the contrary, on the Bateke Plateau in Zaïre and for all the species, the individuals flying between 6 and 8 in the morning are exceptional. From 8 a.m. until 10 a.m. they are still rare except if the morning mist is already dissipated at 8 a.m. and if the sky is very clear[1]. So that, generally speaking it is towards 10 a.m. that the flight begins, and in savannah three groups of species can be distinguished :

- species that fly between 10 a.m. and 3 p.m. with maximum activity about 12 or 1 p.m. : *Scarabaeus kwiluensis* JANSSENS, *Gymnopleurus jacksoni* WATERHOUSE, *G. virens* ERICHSON, *Liatongus interruptus* QUEDENFELD, *Cleptocaccobius youngai* (BALTHASAR) comb. nov.[2]. They are heliophilous species, telecoprid for most of them, or species which are enfeoffed to those telecoprid species (*Cleptocaccobius*),
- species that fly until the end of the afternoon, but whose maximum activity is situated between 10 a.m. and noon. It is the case of *Proagoderus speculicollis* (QUEDENFELD), *Pr. speculatus* D'ORBIGNY, *Onthophagus xanthochlorus* WALTER & CAMBEFORT, *Onthophagus geminatus* D'ORBIGNY,
- species whose flight can be prolonged during dusk and possibly partly at night : *Caccobius histrio* BALTHASAR, *Onthophagus impressicollis* var. *circuitus* D'ORBIGNY, *Pedaria taylori* WATERHOUSE, *P. rohani* BOUCOMONT.

In the forest, where the variation amplitudes of climatic factors are less important than in the savannah, and where population densities are lower, it is not possible to disclose several groups.

1.5. Essential factors determining the flight activity

According to TRIBE (1976), for the diurnal or crepuscular species, the essential factor that regulates the flight activity (time and duration) is the temperature. The activity of the species studied by this author is thus analysed with only taking account this factor, setting out the respective thermic preferendums of those species.

(1) The tabular surface of the Plateau is situated 700 m high and in this region it looks down upon the Congo river from more than 350 m. Besides, this surface is dotted with swamp hollows. So many factors that favour the morning mist forming, and this mist is very frequent (even daily from June to September).

(2) Following the recent creation of the genus Cleptocaccobius CAMBEFORT, this new combination is established from taxonomic considerations given by CAMBEFORT (1979, 1984) on the genus Caccobius.

In fact, if temperature is effectively an important factor - which must however be taken into account with the hygrometry linked to it - it is not the only factor that intervenes. As a consequence the field observations should not be explained with this only factor.

So, luminosity and sunlight must be considered. These factors are fundamental for a lot of savannah species belonging to telecoprid tribes (*Scarabaeini*, *Gymnopleurini* and *Sisyphini* mainly) as well as for certain *Oniticellini* or even *Onthophagini*. Thus on the Bateke Plateau in Zaïre, with a same morning temperature, *Pachylomera femoralis* KIRBY will be seen flying quite earlier (as soon as 8 a.m.) if the sky is completely clear. Species like *Scarabaeus kwiluensis* JANSSENS, *Gymnopleurus jacksoni* WATERHOUSE, *G. virens* ERICHSON will come more numerous on a fresh dung dropped towards noon if there is sunshine.

Another factor wich intervenes, with a delayed action so to speak, is the last rainfall. During the harvestings in the field, we can observe empirically that a day after a rainfall the apparent density of population seems higher for the most common species; in reverse the individuals become less numerous after two or three days without rain. This factor can also intervene to compensate the temperature and luminosity factors : after two or three days rainfall, for such or such a species, the minimum limit-value of these two factors could be lowered. We have there a good example of interaction between ecological factors. Finally, the following hypothesis can be put forward : if some species are both diurnal and nocturnal, this particularity maybe represents an adaptative response to the frequency of rainfalls. The species that are strictly nocturnal and fly during the first part of the night cannot take flight during 48 or 72 consecutive hours if daily rainfalls happen two or three successives night starting as soon as 6 or 7 p.m. as it often happens in these latitudes. On the contrary an indifferent species will be able to take again its flight activity during the day.

As for the flights duration and the frequency of the re-taking flight, they can be linked :

- to food factors : density of attractive sources, nature, quantity, relative freshness,
- to biotic factors : intra or interspecific competition,
- to edaphic factors (for telecoprid and paracoprid species) : texture of the substratum on which the fecal material is explored,

- to the very ethology of the species : for example, *Sisyphus crispatus* GORY and *Gymnopleurus jacksoni* WATERHOUSE show frequent retaking flight because, even without any competition or temptation to hide the ball, they often abadon it a while after the beginning of its transportation (WALTER, 1980).

Finally, it is necessary to remark that the adjective *diurnal* or *nocturnal* applied to a given species only concerns its flight activity and not its activity in general, that is to say the activity related to achieve its trophic and breeding needs mainly. Thus, for a nocturnal species, once the stercoral mass is discovered and accepted, its exploitation and subsequent activities will continue beyond the night, and sometimes in full daylight; it fell to our lot to observe in full sunshine (more than 100,000 Lux) a she-*Catharsius brevicornis* FELSCHE, a nocturnal paracoprid species, that was busy continuing or take up again reserving some dung, a reserving that had probably started the previous night; every time the insect got out of its burrow (or future nest) it was submitted straight away to sun rays and it showed no particular haste, no hesitation that could be interpreted as a reaction to avoid the strong luminosity.

2. *Aphodiidae*

On the Bateke Plateau in Zaïre and in gabonese forest as well, we observed any aphodiine species flying in the day. In those latitudes, the duration of the daily lighting not varying practically during the year, as well as the average temperature, we cannot observe this reversion of activity time according to the seasons set out by LANDIN (1968) and concerning some holartic aphodiines. All the species are then nocturnal.

The nocturnal flight can take place till the morning for some species such as *Pleuraphodius levis* (PAULIAN) or *Trichaphodius humilis* (ROTH); yet, for a majority of species, the flight is scarcely prolonged beyond midnight. But what is characteristic in this group is the extraordinary velocity showed by the aphodiines during the few minutes following the coming of complete darkness. Hundreds of individuals belonging to several species can then be seen converging towards the same bait. Those individuals then react very rapidly to two sorts of stimulus : a photic stimulus that set them in flight, and an olfactive one that immediatly directs the flight.

The arrival on an excrement is immediatly followed by the going deep into it; probability of a retaking flight is very feeble compared to what can be observed for the *Scarabaeidae* when the attractive source is the object of fierce intra or interspecific competition. It results that this common taxis towards the same stercoral mass - movement that confines to gregarious behaviour - leads to a self-limitative effect in the meaning of CHAPMAN (1928); more specially as the interspecific competing effects are added to this homotypical reaction, since it is in fact a plurispecific gregarious behaviour. This self-limitation does not show itself as it does for *Tribolium* for example, insects for which many generations can follow another in the same microbiotope; but rather owing to the number of individuals that invest the dung, the individuals that come to reproduces themselves there will be at the origin of a larval descent numerously more important; the competition will continue between these descendants causing a higher mortality rate.

This limitative effect caused by massive movements at well determined moments only reduces the limits within which an excrement is exploitable, limits which are very narrow because hydrous exigencies as LUMARET (1975) showed it. The massive movements and the brief exploitability period of the excrement have then negative effects, that, when they are superposed, lead to an underexploitation of the available excrement; which permits *Scarabaeidae* that are less exigent to some extent to benefit from it.

3. *Trogidae*

The flight is nocturnal for the four *Trox* species we collected in Zaïre and Gabon. For the two species of the Bateke Plateau in Zaïre, *Trox pusio* KOLBE and *T. melancholicus* FAHRAEUS, it takes place during all the night, that is to say both during the hottest and the coldest hours of the night : the temperature factor seems not to be a determinant factor.

The density of population being always feeble, it is not possible to evaluate for this group the frequency of the re-taking flight. But observations from *T. melancholicus* breeding in terrarium permit to think that the going out are less frequent than for the *Scarabaeidae*.

CONCLUSION

If at the level of some tribes of *Scarabaeidae* we can disclose general facts such the nocturnal character of the *Coprini* and *Onitini*, or the diurnal character of the *Oniticellini*, at the level of other tribes or their different genus this generalization is no longer possible.

Also at the level of forest and savannah faunas, we cannot apply to tropical Africa the principles of HALFFTER & MATTHEWS (1966) according to which there would be quantitative predominance of nocturnal species in forest areas and predominance of diurnal species in open biomes.

At the level of species the factors that condition the flight activity must be appraised in the context of local biotope where such and such a species is studied. In fact the characteristics of the flight of a local population can be different, for the same species, from another local population whose territory is biogeographically quite different from that of the first one. The diurnal *Gymnopleurus virens* ERICHSON supplies us an example. The austral african population studied by TRIBE (1976) shows two daily periods of flight : the first one very early in the morning, the second one in the afternoon, these two periods being separated by a period of inactivity almost total during the hottest hours of the day. But in Central Africa, we personally observed that the Bateke Plateau population shows only one daily period of flight activity, with the maximum activity during the hottest and sunniest hours. Thus, for the first population, high local temperatures intervene as a limitative factor. For the other population, on the contrary, the maximum values that the temperature presents do not appear as a limitative factor; rather minimal values intervene, with important interaction of another factor, the luminosity.

The comparative analysis of the conditions that determine the flight of several populations of the same species permit then, as for other ethological characters, to evaluate the plasticity or the ecological valence of that species.

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