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ECOLOGY OF DUNG BEETLES IN THE FRENCH MEDITERRANEAN REGION (COLEOPTERA: SCARABAEIDAE)

Jean-Pierre Lumaret
& Alan Kirk

Laboratoire de Zoogéographie
Université Paul Valéry
B.P. 5043
34032 Montpellier cedex (France)

RESUMEN

Si no fuera por la actividad de los insectos escarabeidos coprófagos, en las tierras bajo pastoreo el estiércol podría convertirse en el cuello de botella en el proceso de reciclaje de la materia orgánica.

Los estudios origen de este trabajo han sido realizados en el Languedoc, región meridional francesa situada sobre el litoral del Mediterráneo. La mayor parte de las estaciones de estudio estuvieron localizadas en el sector de "garrigues" (formación mediterránea de matorral esclerófilo), correspondiente a una situación kárstica de baja altitud (200 a 400 metros), con una vegetación dominada por la encina verde (*Quercus iles* L.), en condiciones climáticas mediterráneas típicas (invierno fresco y húmedo, verano cálido y seco).

Los escarabeidos coprófagos están organizados en comunidades de especies emparentadas, del mismo nivel trófico, que juegan unas en relación a las otras papeles complementarios en la utilización de las deyecciones animales. Hemos estudiado: 1) como la estructura de las comunidades se modifica a través del año y a lo largo de dos gradientes de vegetación; 2) cuales son las estrategias desarrolladas por los insectos para utilizar los excrementos; 3) como la tasa de dispersión de la boñiga está determinada por la distribución espacial de los insectos y su nivel de actividad.

Dispusimos trampas atrayentes de un modelo estándar en diferentes lugares a lo largo de dos gradientes de la misma serie de vegetación, gradientes que se distinguen el uno del otro por la naturaleza del suelo, y que en ambos casos comprenden de los pastos más abiertos al bosque más cerrado. Resalta en forma muy neta que la estructura de la vegetación controla estrechamente la riqueza de las comunidades de escarabeidos coprófagos a lo largo de las sucesiones vegetales. Sin embargo, a la inversa de lo que se ha observado en otras regiones, en especial en las tropicales, no se observa la coexistencia de dos grandes grupos faunísticos, uno de lugar abierto y otro de bosque. En nuestra área de estudio la cubierta forestal juega simplemente un papel de filtro en relación a los insectos: sólo las especies más abundantes en medio abierto pueden penetrar al bosque. En estas circunstancias el número de individuos de las pobiaciones bajo cubierta forestal se mantiene muy bajo.

Otro factor determinante de las comunidades de escarabeidos coprófagos, es la textura y la capacidad de los suelos para retener agua. Los suelos mejor drenados son en general los más favorables y las estaciones de trabajo correspondientes incluyen una fauna rica y variada. A otra escala, la temperatura juega un gran papel y podemos ver, incluso sobre cortas distancias, una modificación en la composición de las comunidades sin que el funcionamiento general del sistema sea perturbado. Lo más frecuente es que los cambios se efectúen por reemplazamiento de unas especies por otras en el seno del mismo "guild" de insectos, así como por modificaciones de las frecuencias relativas de las especies.

Desde un punto de vista funcional, dos tipos principales de excrementos existen en la región estudiada. Uno representado por las boñigas de vaca, el otro por las bolitas de oveja. Las boñigas, utilizables en la superficie del suelo durante un período bastante largo, son empleadas en todas las estaciones por las grandes especies cavadoras (*Geotrupes, Copris, Bubas*) o de tallas media (*Onthophagus*) y por varios *Aphodius* que oviponen en el interior del excremento, en la parte donde la humedad es óptima. Las larvas de los *Aphodius* emigran progresivamente hacia la base del excremento y la ninfosis se verifica en el suelo.

Las bolitas de oveja constituyen por el contrario una fuente de alimento extremadamente transitoria que se seca muy rápido, entre algunas horas y pocos días según las circunstancias. En estas condiciones los escarabeidos han desarrollado diversas estrategias para utilizar este tipo de excremento. Así los *Aphodius* oviponen directamente bajo el excremento en el contacto con el suelo y las larvas a su emergencia cavan ellas mismas una galería que aprovisionan con los excrementos. En ciertos casos la hembra puede cavar pequeñas galerías ramificadas en las que ovipone y que antes habrá aprovisionado con alimento.

La mayor parte de los insectos escarabeidos ovipone en la primavera o en el otoño es decir durante los períodos templados y húmedos del año. La actividad en verano es por el contrario muy reducida, en consecuencia, en la región mediterránea la tasa de utilización de los excrementos es variable a lo largo del año y

éstos pueden permanecer en la superficie del suelo durante varios meses. Sin embargo, la diversidad de los "guild" de escarabeidos coprófagos y su abundancia son tales que las cantidades de excremento que permanecen sin usarse son reducidas, lo que limita la tasa potencial de infección del ganado por diversos parásitos.

SUMMARY

Several studies were carried out in Languedoc, a french mediterranean province in the South of France. Most of the sites studied were located in the Garrigue zone, a typically low karst, under mediterranean climatic conditions (cool moist winter and warm dry summer).

Dung beetles were organized into ecological communities of related species playing a complementary role in the utilization of cattle droppings. The following points were studied: (1) how the structure of dung beetle communities evolves throughout the year in mediterranean conditions; (2) what strategies are developed in the use of dung; (3) how the spatial distribution of insects modifies the rate of dung dispersal.

Dung baited pitfall traps of standard design were set up along two vegetation gradients, going from the most open to the most forested habitat. It appeared very clearly that the vegetation structure determined to a very large extent the level of dung beetle community richness in each of the six stages defined along the vegetation succession. But, conversely to that pointed out under other climates, the coexistence of two distinct faunistic groups, one from open areas and the other from forests, was not observed there. The vegetation cover acts like a filter which only lets several ubiquitous open area species through the undergrowth but, at the same time, drastically limits their numbers.

On a smaller scale, the spatial distribution of dung beetles is also controlled by the texture and the capacity of soils to retain water. On a regional scale, temperature is determinant, and a progressive replacement of typical mediterranean communities by a mixture of species which are more tolerant to cold is observed, sometimes over a short distance.

Two principal models of faeces were defined, one represented by cow pads and the other by sheep droppings. Because they remain usable over a long period, cow pads are used in all seasons by burying species of large (e.g. *Geotrupes, Bubas, Copris*) or medium size (*Onthophagus*), and by several *Aphodius* which lay their eggs inside them. Sheep droppings, on the contrary, represent a transient source of food which dries within several hours or days. Consequently it is observed that the insects have developed diverse behaviour to remove this material as quickly as possible from other consumers and from the unfavourable effects of climatic factors.

Most of the *Aphodius* oviposit under the droppings and when the larvae emerge, they dig immediately themselves a narrow burrow and fill it with dung.

Most of the insects oviposit in spring or autumn and reduce their activity in summer. Consequently the rate of dung dispersal over the year is uneven and dung may remain on the ground surface for several months. But diversity of the dung beetle guilds and abundance of the insects contribute, in most cases, to maintaining a high rate of dung dispersal and thereby a low level of cattle parasites.

INTRODUCTION

In pastures supporting high populations of large herbivores, organic material such as dung represents a potential bottleneck in the recycling process if it is not decayed by microflora and numerous Invertebrates. For example, a single cow can produce some 8 tons of dung each year. This feeding source, even enough abundant, may be intermitted and transient. That is the case when dung beetles, which are the essential insects in that recycling process, immediately take possession of a large part of the faeces before they dry. Without insects, cow pads or horse droppings may remain longer on the ground (Lumaret 1986).

Scarabeid beetles constitute an ecological group divided in to several guilds. In each site they are organized into communities of related species which possess the same trophic level and exploit the same class of environmental resources but use complementary strategies for their development. Obviously, dung beetles are of great interest for the ecologist who looks at dynamics and management of ecosystems.

The ecology and community structure of dung beetles are well known in northern Europe (Landin 1961, Koskela and Hanski 1977, Hanski and Koskela 1978, Hanski 1979, 1980, and 1986, De Graef and Desière 1984), and in several tropical regions (Walter 1978, Cambefort 1982 and 1983, Peck and Forsyth 1982, Hanski 1983, Kohlmann and Sanchez Colon 1984). Papers about ecology of dung beetles in countries with mediterranean-type climates –with a cool moist winter and a warm dry summer– are quite numerous (Lumaret 1978, Martin-Piera 1982, Mesa i Pongiluppi 1985); however very few concern the structure of insect communities (Nealis 1977, Lumaret 1983, Ridsdill-Smith *et al.* 1983, Ridsdill-Smith and Hall 1984).

Communities are constituted by many species, the diversity of which depends on climatic conditions and latitude. In northern Europe 40 or 50 species only are found (Landin 1961), whereas more than 100 occur in the South of France (Lumaret 1978), 143 in Zaire (Walter 1978) and 286 in Ivory Coast (Cambefort 1983). Their geographical distribution depends also on diverse ecological factors; usually all the authors agree with the idea that the richness of dung beetle communities is higher in open fields than in forests (Nealis 1977, Walter 1978, Lumaret 1983, Hanski 1983, Peck and Howden 1984).

The aim of the present study is to show: (1)- how the structure of dung beetle communities evolves throughout the year in mediterranean climatic conditions; (2)- what strategies are developed in the use of dung; (3)- whether the spatial distribution of these insects modifies the rate of dung dispersal.

I. THE STUDY REGION

a) LOCALITY

The Languedoc region is located in the south of France at the extreme south east of the Massif Central as a prolongation of the limestone Grands Causses (Causse Méjean, Causse du Larzac) and the granite Cevennes. It is like a vast amphitheatre turned towards the Mediterranean, consisting of a succession of Jurassic and Cretaceous plateaux, alternating with small synclinal depressions occupied by younger deposits. The coastal plain is formed of Pliocene and Quaternary sediments and joins the Camargue delta of the Rhône river.

b) NATURAL DIVISIONS

It is possible to divide up the region into 4 great natural areas:

- The Great Causses, vast limestone plateaux (altitude between 800-1000 m);
- The Garrigue, typically on mediterranean karst, which extend up to an altitude of about 100-400 m;
- The Camargue, and the edges of the lagoons, situated at sea level;
- The sand dune belt along the shore line.

c) SOILS

Soils on compact karst limestone are generally red with a brown forest soil on the surface; on soft or flinty limestone brown rendzine soils are formed; finally on stony limestone red washed out iron bearing soils are formed (Rapp and Lossaint 1981).

In the Camargue the soils are of a sedimentary origin and are essentially of a sandy clay nature.

d) CLIMATE

Mediterranean France is a mild region. The climate of the Montpellier zone (Hérault) corresponds to the cool sub-humid Mediterranean type (Emberger 1955) with a pluviothermic quotient of 86 (Nahal 1981). The annual mean temperature is 14.4°C, the mean maximum temperature of the warmest month (July) is 31.4°C and the annual mean precipitation (over 60 y) is 760 mm fluctuating greatly between years. The distribution of precipitation is characteristic of a mediterranean climate with 2 humid phases (autumn and spring) and a dry period of 2 to 3 months (summer).

e) VEGETATION

Quercus ilex forest (the holm-oak is a broad leaved evergreen sclerophyllous tree) is the climax formation of the region. This formation is now found only very locally as it has been replaced over large areas by the "garrigues" of mixed *Q. ilex* and *Q. coccifera,* themselves transformed by grazing into *Brachypodium ramosum* pastures. To the north of Montpellier *Q. ilex* is mixed with a deciduous species *Q. pubescens.* Most of the cultivated land is occupied by vineyards.

In the Camargue the vegetation is different, consisting mainly of grasses and low trees, *Tamarix gallica* growing on a humid silty clay sand.

f) ANIMAL PRODUCTION

Sheep rearing is an ancient practice and dominates on the Causses and in the Garrigue of Languedoc. There are an estimated 35,000 sheep running the Garrigue of the Montpellier region, every flock consisting of about 200 head. During summer most of the flocks leave the dry, low altitude Garrigue for higher areas on the Causses and the Cevennes.

On the coastal plain and in the Camargue, cattle are more numerous (several 1,000 s). The herds consist of 100-300 head which are used only for bull fighting.

II. THE DUNG BEETLE SPECIES PRESENT IN LANGUEDOC

Ninety eight dung beetle species are recorded from the Languedoc. Their distribution is not uniform, reflecting the diversity of localities found there (Tables 1 and 2).

a) THE CAUSSES

Sixty species are present on the Causses which constitute an habitat with a particularly homogeneous fauna. Some species, e.g. *Copris umbilicatus* Ab. de P., are found there at the western limit of their distribution. Others, e.g. *Gymnopleurus sturmi* Mc. L. and *Euonthophagus gibbosus* (Scriba), are only found in the most arid and denuded parts of the Causses.

The western part of the Larzac is lower (600-800 m) and both more wooded and humid, as it is under the influence of Atlantic depressions. *Trypocopris pyrenaeus* Charp. is found there. By contrast in the most southerly zone, which is drier and deeply cut by sheltered valleys, several other species are found. They constitute normally a part of the most characteristic communities in the Garrigue, e.g.

Table 1

Size and mean dry weight (10 beetles) of dung beetles present in the Languedoc region of Mediterranean France.

	Dunes	Camargue	Garrigue	Causses	Species cited in the localities studied	Length (mm)	Mean dry weight (mg)
SCARABAEIDAE:							
Scarabaeus sacer L.		+				28-32	
Scarabaeus typhon Fischer			+		+	20.0	353.6
Scarabaeus pius Illiger			+			20-28	
Scarabaeus semipunctatus Fabr.	++++				+	18-27	
Scarabaeus laticollis L.			+++		+	20.0	172.9
Gymnopleurus sturmi Mc L.		+	+	+	+	10-13	
Gymnopleurus mopsus (Pallas)		+	+			7-14	
Gymnopleurus flagellatus (Fabr.)			+		+	9.7	102
Sisyphus schaefferi (L.)			+++	++	+	9.0	29.0
Copris lunaris (L.)		+	+	++		18.0	228.0
Copris umbilicatus Ab. de P.				++	+	17.0	242.7
Copris hispanus (L.)		++	+++		+	19.0	513.3
Onitis belial Fabr.		+				16-27	
Bubas bison (L.)	+	+++			+	17.0	216.0
Bubas bubalus (Ol.)		++	+++		+	18.0	197.6
Euoniticellus fulvus (Goeze)		+++	+++	++	+	9.0	25.1
Euoniticellus pallipes (Fabr.)		+	+	+		6.5-10	
Caccobius schreberi (L.)		++	++	++	+	5.5	7.1
Euonthophagus amyntas (Ol.)			++	+	+	7.5	27.0

Table 1 (continued)

	Dunes	Camargue	Garrigue	Causses	Species cited in the localities studied	Length (mm)	Mean dry weight (mg)
Euonthophagus gibbosus (Scriba)			+	++	+	10.5	22.5
Onthophagus taurus (Schreb.)		+++	++	+	+	8.5	32.4
Onthophagus illyricus (Scop.)		+	+			5.5-11.5	
Onthophagus emarginatus Mulsant		++	+++	+	+	5.5	7.6
Onthophagus furcatus (Fabr.)	+	+	++	+	+	3.7	3.7
Onthophagus verticicornis (Laich)			+++	++++	+	7.6	18.7
Onthophagus semicornis (Panz.)		+			+	5.5	10.0
Onthophagus grossepunctatus Reitt.		+	++	+++	+	4.5	5.0
Onthophagus ruficapillus Brullé		+++	+	++	+	4.5	5.5
Onthophagus ovatus (L.)		+	++	+		4.4	5.7
Onthophagus joannae Goljan			+++	++++	+	4.7	6.2
Onthophagus coenobita (Herbst.)	+	++	+++	++	+	7.1	21.8
Onthophagus opacicollis Orb.		++	+			5-8	
Onthophagus similis (Scriba)				++		4-7	
Onthophagus fracticornis Preyssl.				+++	+	8.5	10.0
Onthophagus lemur (Fabr.)		++	++++	++++	+	6.5	13.4
Onthophagus maki (Ill.)			++	+	+	5.5	10.5
Onthophagus vacca (L.)	+++	++++	+++	++++	+	10.0	41.2
Onthophagus nuchicornis (L.)	++	+++	+			6-9	
APHODIIDAE							
Aphodius (Colobopterus) erraticus (L.)		++	+++	+++	+	7.5	8
Aphodius (Colobopterus) scrutator (Herbst.)		+	+	+++	+	11.1	40.8

Table 1 (continued)

	Dunes	Camargue	Garrigue	Causses	Species cited in the localities studied	Length (mm)	Mean dry weight (mg)
Aphodius (Colobopterus) subterraneus (L.)		++	++	+++	+	6.9	7.4
Aphodius (Otophorus) haemorrhoidalis (L.)		+++	++	++	+	4.6	4
Aphodius (Ammoecius) elevatus (Ol.)		++	+++		+	5.5	6.5
Aphodius (Plagiogonus) putridus (Fourcr.)			+	+		2.5-3	
Aphodius (Acrossus) luridus (Fabr.)		++	++++	++++	+	8.2	12.1
Aphodius (Acrossus) depressus (Kug.)				+		6-9	
Aphodius (Acrossus) rufipes (L.)				+		11-13	
Aphodius (Biralus) satellitius (Herbst.)		++	++			5.0	22.7
Aphodius (Orodalus) coenosus (Panzer)			+	++		3.5-5	
Aphodius (Orodalus) paracoenosus Balth. Hrub.		+++	+++	++	+	3.6	2.3
Aphodius (Orodalus) pusillus (Herbst.)		++	++	+++	+	3.0	1.3
Aphodius (Nimbus) obliteratus Panz.		+	+			4.5-6	
Aphodius (Nimbus) contaminatus (Herbst.)		++	+	++		5-6.5	
Aphodius (Volinus) equestris (Panz.)				+		4.5-5	
Aphodius (Volinus) cervorum Fairm			+			4-5	
Aphodius (Volinus) distinctus (Mull.)		+++	+	++	+	4.3	2.8
Aphodius (Melinopterus) sphacelatus (Panz.)		++	+	+	+	5.4	3.7
Aphodius (Melinopterus) prodromus (Brahm)		++	+	++	+	6.1	4.9
Aphodius (Melinopterus) reyi Reitt.		+	+			4-5	
Aphodius (Melinopterus) consputus Creutz.		++	+	+++		3.9	1.8
Aphodius (Melinopterus) tingens Reitt.		++	+	+	+	4.5-6	
Aphodius (Nobius) bonnairei Reitt.		+	+			3.2-3.5	
Aphodius (Amidorus) porcus (Fabr.)		+				5-6	
Aphodius (Amidorus) thermicola Sturm.			+			6-6.7	

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Table 1 (continued)

	Dunes	Camargue	Garrigue	Causses	Species cited in the localities studied	Length (mm)	Mean dry weight (mg)
Aphodius (Trichonotulus) scrofa (Fabr.)		++	++	++	+	3.2	1.4
Aphodius (Emadus) quadriguttatus (Herbst.)		+	++	+++		4.4	2.2
Aphodius (Emadus) quadrimaculatus (L.)			++	+++	+	3-3.5	0.8
Aphodius (Emadus) biguttatus Germar.			+++	+++	+	2.8	0.6
Aphodius (Mecynodes) striatulus Waltl.		+	+			3	
Aphodius (Esymus) merdarius (Fabr.)		++	+		+	4.5	0.9
Aphodius (s. str.) scybalarius (Fabr.)		++	++			6.4	6.8
Aphodius (s. str.) fimetarius (L.)		++	+	++	+	6.5	9.9
Aphodius (s. str.) aestivalis Stephens		+				6-9	
Aphodius (Loraphodius) suarius Fald.		+				5-7	
Aphodius (Agrilinus) constans Duft		++	+++		+	5.5	4.6
Aphodius (Oromus) alpinus (Scop.)				+		5-7	
Aphodius (Bodilus) immundus Creutz.		+++	+			5-6	
Aphodius (Bodilus) nitidulus (Fabr.)				+++	+	5.7	3.3
Aphodius (Bodilus) ghardimaouensis Balth.		++++			+	4.5-5.5	
Aphodius (Bodilus) lugens Creutz.		++				7-8.5	
Aphodius (Bodilus) rufus Moll.				++		5-7	
Aphodius (Nialus) sturmi Harold		++				3.1	0.9
Aphodius (Nialus) plagiatus (L.)		+				3-4	
Aphodius (Nialus) varians Duft.		+++	+	+		4-6	
Aphodius (Nialus) lividus (Oliv.)		+				3-6	
Aphodius (Calamosternus) granarius (L.)	++	+++	++++	++++	+	4.0	3.4
Oxyomus silvestris (Scop.)		++	+	+	+	3.0	1.1
Pleurophorus caesus (Creutz.)		+				2.5	3.3

Table 1 (end)

	Dunes	Camargue	Garrigue	Causses	Species cited in the localities studied	Length (mm)	Mean dry weight (mg)
TROGIDAE							
Trox perlatus (Geoff.)		+	++	+++	+	7.0	28.1
Trox hispidus (Pontopp.)		+	+	++	+	5.5	13.2
GEOTRUPIDAE							
Typhoeus typhoeus (L.)		+	+		+	12.8	156.0
Geotrupes mutator Marsh.		+	+	++		15-24	
Geotrupes niger Marsh.		++	+++	+++	+	19.0	143.0
Geotrupes spiniger Marsh.	+	+++	+	++	+	22.0	386.9
Anoplotrupes stercorosus (Scriba)				++		12-19	
Trypocopris pyrenaeus Charp.				+		12-20	
Trypocopris vernalis (L.)				+++	+	15.9	119.5
Thorectes intermedius (Costa)		+				11-20	
Total number of species: 98	8	69	71	60			

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Table 2

Distribution of number of dung beetle species in the Languedoc.

	Causses	Garrigue	Camargue	Dunes
Scarabaeidae	23	30	24	6
Aphodiidae	29	35	38	1
Geotrupidae	6	4	5	1
Trogidae	2	2	2	—
TOTAL	60	71	69	8

Onthophagus furcatus (Fabr.), *O. maki* (Ill.), *O. lemur* (F.), *Euonthophagus amyntas* (Ol.) and *Euoniticellus fulvus* (Goeze).

b) THE GARRIGUE

The association of dung beetle species of this limestone part of Languedoc constitutes the most typical fauna of southern France. Despite their dryness the Garrigue has a very high specific richness. The 71 species recorded are nearly all adapted to dry soils and to the occurrence of a summer drought period, occasionally as long as 3 months.

The French guild of telecoprids is not very rich, and it is represented here by 7 species from 3 genera (*Scarabeus, Gymnopleurus* and *Sisyphus*). The paracoprids very largely dominate, with some large species belonging to the genera *Copris, Bubas* and

Geotrupes, and species of much smaller genera such as 2 *Euoniticellus,* 1 *Caccobius,* 2 *Euonthophagus* and 15 *Onthophagus.*

c) THE CAMARGUE AND THE EDGES OF THE LAGOONS OF THE LITTORAL PLAIN

The dung beetle richness of this faunistic region (68 spp. recorded) is certainly connected with the long established animal production, and to the diversity of local conditions. In the driest parts, *O. emarginatus* Muls. is found in abundance. In the other sites however, the well worked, deep and more humid soil allows larger species e.g. *Onitis belial* F., *Bubas bubalus* Ol., *B. bison* (L.) or *Geotrupes spiniger* Marsh to be maintained. They need indeed to dig deep rearing tunnels. Species with central european distribution e.g. *Copris lunaris* (L.), *Aphodius aestivalis* Stephens or *A. scrutator* (Herbst) are equally able to maintain themselves in the Camargue, whereas they are absent normally from mediterranean areas affected by a long summer drought (compensation of ecological factors). The presence in the Camargue of 4 *Aphodius* species of the subgenus *Nialus* shows the occurrence of humid conditions in this area.

d) THE COASTAL DUNES

This faunistic sector constitutes a very fragile zone because it only consists of a narrow band of sand dunes situated between the sea and the littoral lagoons. This natural area, under constant pressure from uncontrolled tourist development, supports only 8 species, amongst which *Scarabaeus semipunctatus* F. is restricted to the area.

III. SPATIAL DISTRIBUTION OF DUNG BEETLES IN THE MEDITERRANEAN GARRIGUE

The western part of the French mediterranean Garrigue is a vast area where the altitudinal, climatic and edaphic diversity define several faunistic sub-units (Lumaret 1978-79 a & b). At the regional level, each faunistic sector appears very characteristic and different from nearby sectors. On a smaller scale however, the diversity between the study sites is extreme. That is due to numerous physical factors which divide each sector into an infinite number of different, but strongly interlocked biotopes, with a north-south altitudinal and climatic axis superimposed on them.

The study of factors affecting the evolution of dung beetle communities has been carried out in the Garrigue (*Quercus pubescens*) (sector Montpelliérais). The experiments were aimed at an understanding of the organization of communities along a vegetation gradient, going from the most open to the most forested habitat.

In such a gradient, the complexity and the thickness of the vegetation increase, but this manifests itself differently according to the nature of the substrate. Six physiognomic levels (stages) forming a structural continuity have been identified on a hard limestone substrate and 6 others on a limestone flint substrate (Fig. 1).

The first vegetation gradient grouped 6 sites with clay soil on a solid fissured limestone, allowing rapid infiltration of water after each rainy period. Under such edaphic conditions, the extreme stages of vegetation are a short pasture of *Brachypodium ramosum* and a dense forest of *Quercus pubescens,* the light at soil level remaining important in the intermediate preforest stages due to a slight low vegetation soil covering.

The second gradient consisted of 6 sites on flinty soil lying on a solid limestone core. This soil type, more acid and more humid, where the water table periodically rises and floods the surface during the rainiest periods of the year, favorises the growth of heaths (*Erica scoparia*). The lower branches of this plant species rapidly block the space and close the habitat. Consequently, the light intensity on the forest-floor is reduced in most of the sites. These branches only disappear by wilting in the final stages of the vegetation succession.

At each of the sites two dung beetle traps of standard design (Lumaret 1979) were set up and examined every 10 days during one year. Ten thousand two hundred and seventy one insects belonging to 36 species were trapped during this period in the 6 sites on hard limestone, whereas only 18 species and 381 individuals were trapped in the 6 sites on flinty limestone, that is 2 times fewer species, 26 times fewer individuals and a biomass 35 times less.

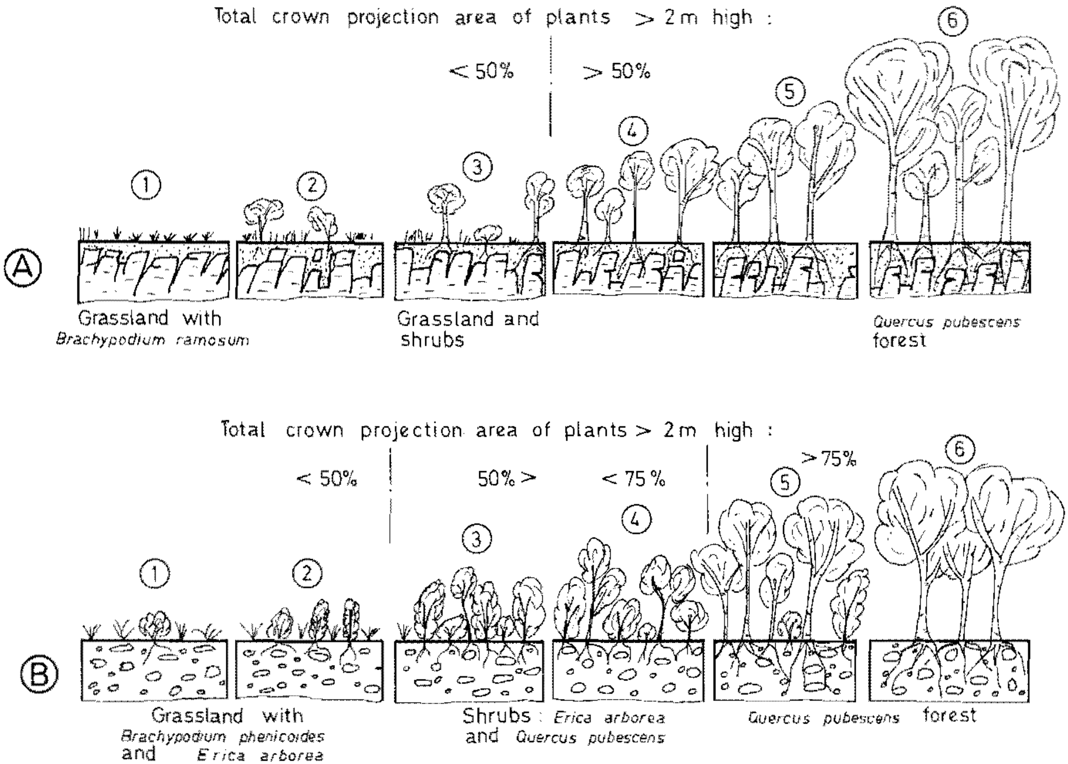

Figure 1

Successive evolutionary stages of vegetation cover (1 to 6) on a hard fissured limestone substrate (A) and on a flinty limestone substrate (B) in Languedoc.

1. INFLUENCE OF THE VEGETATION COVER

The majority of insects react in the same way when faced with the progressive thickening of vegetation which deeply modifies microclimate and more specially light intensity. The sensitivity of each species is nevertheless variable. The Scarabaeini, for example, react much more strongly than the Sisyphini when faced with the closing off of the vegetation canopy (Table 3).

From figure 2, for each of the vegetation successions, great differences appear in species richness between the sites, the most open presenting the highest index of diversity (Tables 4 and 5).

In the succession on hard limestone, only 10 species out of 36 are eurytopic and can colonize both open and forested habitats. They represent 81.1% of the total annual capture for the 6 stages as they nearly always have very large populations. However their distribution is not equal along the vegetation gradient. The meeting of the tree crowns results in more than 50% of the ground being covered leading to a very rapid drop in number and in species richness; the last 2 stages of the succession (n° 5 and 6) contain only 5% of the total insect number of these 10 species; the last stage of the succession (forest, stage n° 6) shows no more than 3 species: *Trox perlatus, O. lemur* and *O. coenobita* (Table 4).

Table 3

Distribution of Scarabaeini and Sisyphini trapped along a physiognomic vegetation gradient (substrate: clay on hard limestone).

Species	Physiognomic stages					
	1	2	3	4	5	6
Gymnopleurus flagellatus	1	0	0	0	0	0
Scarabaeus laticollis	92	98	57	0	0	0
Scarabaeus typhon	2	0	1	1	0	0
Sisyphus schaefferi	190	207	191	37	13	0

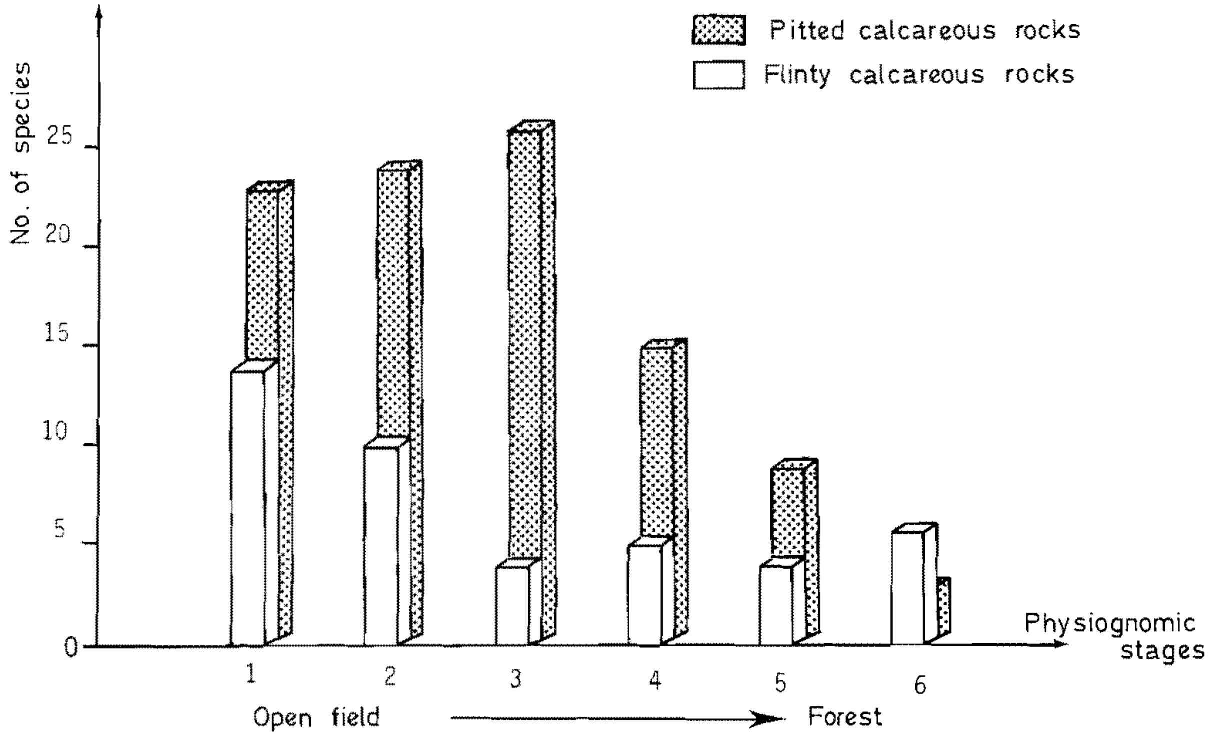

Figure 2

Evolution of the number of dung beetle species as a function of the openness of habitat and of geological substrate (from Lumaret 1984).

Table 4

Relative frequencies and biomass of species at 3 localities of the mixed evergreen/deciduous oak near Montpellier (stages 1, 3, and 6 of the vegetation succession). Substrate: clay on fissured limestone.
Data from a full year of trapping (March 1978 - April 1979).

Species	*B. ramosum* pasture (Stage 1) numbers (%)	*B. ramosum* pasture (Stage 1) biomass (%)	Low garrigue of *Q. ilex* and *Q. pubescens* (tree cover 35%) (Stage 3) numbers (%)	Low garrigue (Stage 3) biomass (%)	*Q. pubescens* forest (Stage 6) numbers (%)	*Q. pubescens* forest (Stage 6) biomass (%)
Trox perlatus	0.11	0.09	0.11	0.18	0.92	1.19
T. hispidus	1.23	0.45	0.24	0.19	---	---
Geotrupes niger	0.11	0.44	0.32	2.67	---	---
Typhoeus typhoeus	0.06	0.24	---	---	---	---
Scarabaeus laticollis	5.13	24.82	1.52	15.34	---	---
S. typhon	0.11	1.10	0.03	0.55	---	---
Sisyphus schaefferi	10.61	8.60	5.10	8.62	---	---
Gymnopleurus flagellatus	0.06	0.16	---	---	---	---
Euoniticellus fulvus	---	---	0.13	0.20	---	---
Copris hispanus	1.06	15.22	0.24	7.19	---	---
Caccobius schreberi	---	---	0.72	0.30	---	---
Euonthophagus amyntas	1.06	0.80	0.03	0.04	---	---
Onthophagus emarginatus	5.75	1.22	0.99	0.44	---	---
O. furcatus	0.16	0.02	0.19	0.04	---	---
O. lemur	41.68	15.60	58.54	45.71	2.75	1.71
O. maki	5.47	1.60	8.84	5.41	---	---
O. vacca	23.97	27.57	0.67	1.60	---	---
O. joannae	0.33	0.06	8.82	3.18	---	---
O. coenobita	0.11	0.07	3.90	4.95	96.33	97.10
O. verticicornis	1.84	1.65	0.40	0.75	---	---
Aphodius subterraneus	---	---	0.03	0.01	---	---
A. haemorrhoidalis	---	---	1.55	0.36	---	---
A. luridus	0.73	0.25	0.83	0.58	---	---
A. paracoenosus	0.06	0.003	0.43	0.06	---	---
A. biguttatus	---	---	0.48	0.02	---	---
A. fimetarius	0.06	0.01	0.13	0.08	---	---
A. constans	---	---	5.61	1.50	---	---
A. granarius	0.22	0.02	0.08	0.02	---	---
Oxyomus silvestris	0.06	0.002	---	---	---	---
Number of species	23		26		3	
Number of individuals trapped	1 790		3 743		109	
Total annual biomass/trap (mg dry wt)	64 095.4		64 227.6		2 357.3	
Shannon H'o Index of diversity	2.58		2.36		0.26	

Table 5

Annual relative frequencies of numbers (Nb%) and biomass (Bm%) of species along the pasture-forest gradient. Substrate: flinty limestone.

	Physiognomic stages											
	1 pasture		2		3		4		5		6 forest	
	Nb%	Bm%	Nb%	Bm%	Nb%	Bm%	Nb%	Bm%	Nb%	Bm%	Nb%	Bm%
Trox perlatus	---	---	21.09	36.43	71.43	82.41	14.29	20.85	36.11	47.47	17.74	28.03
T. hispidus	---	---	0.78	0.63	---	---	---	---	---	---	---	---
Sisyphus schaefferi	5.88	20.39	6.25	6.96	---	---	---	---	---	---	1.61	2.63
Euoniticellus fulvus	1.18	2.21	---	---	---	---	---	---	---	---	---	---
Caccobius schreberi	1.18	0.62	0.78	0.34	---	---	---	---	---	---	---	---
Euonthophagus amyntas	3.53	7.12	---	---	---	---	---	---	---	---	---	---
Onthophagus emarginatus	3.53	2.00	24.22	11.31	---	---	---	---	---	---	---	---
O. furcatus	29.41	8.13	1.56	0.36	---	---	---	---	---	---	---	---
O. taurus	1.18	2.85	---	---	---	---	---	---	---	---	---	---
O. joannae	2.35	1.09	0.78	0.30	4.76	1.21	4.08	1.32	8.33	2.42	---	---
O. coenobita	7.06	11.49	14.06	18.84	9.52	8.52	48.98	55.47	38.88	39.66	40.32	49.42
O. lemur	35.29	35.33	28.91	23.81	14.28	7.86	30.61	21.31	16.66	10.45	19.35	14.58
O. maki	1.18	0.92	1.56	1.01	---	---	---	---	---	---	---	---
O. vacca	2.35	7.24	---	---	---	---	---	---	---	---	---	---
Aphodius sphacelatus	---	---	---	---	---	---	---	---	---	---	1.61	0.34
A. biguttatus	4.71	0.21	---	---	---	---	---	---	---	---	---	---
A. fimetarius	---	---	---	---	---	---	2.04	1.05	---	---	---	---
A. constans	1.18	0.40	---	---	---	---	---	---	---	---	19.35	5.00
Number of species	14		10		4		5		4		6	
Number of individuals	85		128		21		49		36		62	
Annual biomass/trap (mg dry wt)	1 138.0		2 082.4		511.5		943.2		769.5		1 102.8	
Shannon H'o Index of diversity	2.74		2.48		1.28		1.73		1.79		2.08	

In the case of pastures, the telecoprids (*Scarabaeus, Sisyphus* and *Gymnopleurus*) play a considerable role because, although they constitute only 15.9% of the total capture annually, they represent 34.7% of its biomass. Similarly the paracoprid *Copris hispanus* (L.) although being relatively scarce (1.1% of the total), constitutes 15.2% of the total biomass. Conversely, the *Aphodius* spp. remain always unimportant in the Garrigue both in number (1.1%) and biomass (0.3%). The highest annual biomass (27.6%) is constituted by *O. vacca* (L.) which represents nearly a quarter of the total insect number; *O. lemur,* the species with the most numerous individuals (41.7%), represents 15.6% of the annual biomass.

As soon as the area closes (stage n° 3) the number of telecoprids diminishes (6.7%) as does their biomass (24.5%) (Table 3).

In the forest, the insect biomass is 25-30 times lower than in open areas. *O. coenobita* very largely dominates, with 96.3% of numbers and 97.1% of annual biomass.

On flinty limestone the diminution of species richness and of numbers of dung beetles is very rapid because it begins as soon as the appearance of the first heaths (stage n° 2, Fig. 1B). The obstruction of the lowest levels by dense vegetation only clears in the last stages of the vegetation succession. This occurs when heathers wilt and disappear following the growth of the trees. The clearing of the forest-floor allows dung beetles to reappear. This explains the increase in diversity of dung beetles recorded from the most heavily forested stages (Table 5). Here again, *Onthophagus coenobita, O. lemur* and *Trox perlatus* are among the best distributed species along the vegetation gradient.

When compared with the biomass obtained for each of the stages on hard limestone, biomass of the dung beetles trapped on flinty limestone shows very important differences, especially for the first stages of the vegetation succession. Thus, between *Brachypodium ramosum* pastures on hard limestone and *B. phoenicoides* ones on flinty limestone, the biomass becomes about 56 times lower (from 64.1 mg to 1.1 mg). This biomass ratio is maximum for the third stage (=to 125.5) because, on flinty limestones, the cover of the habitat by heath (*Erica scoparia*) only allows 4 species of dung beetles to colonize such a biotope, each being represented by a very small number of individuals. The differences between the two series of vegetation narrow later, biomass reducing considerably in all cases whatever the substrate, as soon as the closing off of the habitat becomes too great. For the most heavily forested cover (stage n° 6), the difference in annual biomass between the series on hard limestone and flinty limestone is the least marked (2,358 mg and 1,103 mg respectively).

In conclusion, it appears very clearly that the vegetation structure determines to a large extent the level of dung beetle community richness for each of the stages of a vegetation succession. But contrarily to what is observed under other climates and, in particular, in the tropical region (Howden and Nealis 1975, Walter 1978, Peck and Forsyth 1982) neither the coexistence of 2 distinct faunistic groups (one from open areas and the other from forests) nor a clear cut off between the communities from the closed off areas and those of the open areas are observed. Vegetation cover acts somewhat like a filter which only lets several ubiquitous open area species through the undergrowth but, at the same time, drastically limits their numbers.

2. INFLUENCE OF SUBSTRATE

On examining the faunistic composition of homologus localities, with the same vegetation structure but differing from the point of view of parent-rocks, great qualitative and quantitative differences are observed. Thus, when the faunas of pastures on hard limestone and flinty limestone are compared (column 1 of Tables 4 and 5), it is observed that some genera are totally missing on flinty limestone and that the species, common to the 2 sites, represent 20 times fewer individuals on flinty limestone than on clay. This extremely rigorous sorting between the dung beetles which, for the most part, are burying species, is due to a difference in the mode of soil drainage. Whilst the hard limestone localities get dry very quickly after a rainy period, in those on flinty limestone the water table rises periodically to the surface. This difference in speed of water percolation is fundamental because, for numerous species which nest inside the soil, the capacity of a soil to retain water, the depth of saturated horizons and the duration of this saturation will determine success or failure of reproduction. A soil which remains saturated with water too long during the reproductive period will be very likely unfavourable for most species. Those which can cope with such conditions cannot build up large numbers because they have a very high larval mortality.

The substrate texture also controls the spatial distribution of dung beetles. It is particularly clear in the case of the ball rollers observed in the south of France (Scarabaeini, Gymnopleurini, Sisyphini). For these, a succession of species is observed from the dunes at the edge of the sea to the Garrigue on clay soil (Table 6). Thus, *Scarabaeus semipunctatus* is confined to the sand dunes along the Languedoc littoral. In the Camargue, but more especially in Corsica, this species is replaced inland by *S. sacer* L. which prefers an equally light but slightly more compact and finer soil (silty-sand soils along the edges of streams, for example). In such a habitat, *S. laticollis* L. and *Sisyphus schaefferi* (L.) may occur but these species are found especially in the Garrigue on compact clay soil, with *Scarabaeus typhon* F. and diverse *Gymnopleurus* spp.

Table 6

Distribution of ball rollers relative to soil texture.

Species	Texture		
	Sandy	Silty	Clay
Scarabaeus semipunctatus Fabr.	++		
S. sacer L.		++	
S. typhon Fabr.			++
S. pius Illiger			++
S. laticollis L.		+	++
Gymnopleurus sturmi Mc L.			++
G. mopsus (Pallas)			++
G. flagellatus (Fabr.)			++
Sisyphus schaefferi (L.)		+	++

3. INFLUENCE OF TEMPERATURE

The sensitivity of dung beetles to this factor is so high that a progressive replacement of typical mediterranean communities by a mixture of species more tolerant to cold is observed along the strong thermal gradient occurring from the coast to the Causses plateaux (about 80 km, with a 6°C difference between average January temperatures).

In the Garrigue, this replacement can also be observed over short distances (several kilometers) where local microclimate variations do exist. The variation concerns the frequency of the most thermophilic species to such an extent that the community structure of dung beetles in those localities is deeply modified. It is the case when the site of Viols-le-Fort (site 1, alt. 240 m) and the site of Causse-de-la-Selle (site 2, alt. 245 m), only 10 km apart are compared. These localities which have the same aspect, the same degree of openness and the same soil characteristics, differ only by an average temperature which is slightly lower in Causse-de-la-Selle (Table 7). Species which were already at the limit of their distribution in site 1, such as *Scarabaeus typhon, Copris hispanus* or *Euonthophagus amyntas* disappear in site 2. In the same way the frequency of *Onthophagus lemur* strongly diminishes from 58.5% of total captures in site 1 to 15.5% in site 2. Conversely the frequency of the more montane distributed species increases from site 1 to site 2. It is the case for *O. joannae* (increase from 8.8% to 26.1%) and more especially for *O. verticicornis* (increase from 0.4% to 32.8%). The difference in biomass between the 2 sites (64,227.6 mg on average/trap at site 1 against 74,197.8 mg at site 2 is due to the presence of a slightly larger proportion of *S. laticollis* and *O. verticicornis* at Causse-de-la-Selle, which very largely compensates for the absence of *C. hispanus* at this site.

IV. PHENOLOGY OF DUNG BEETLES IN SOUTHERN FRANCE

The adults of many dung beetles species are active for only limited periods in the year and at specific times of the day, whatever be the climatic area. Several dung beetle pitfall traps have therefore been set up in the different sites, on the Causses and in the

Table 7

Comparison of 2 Garrigue localities near Montpellier, having the same degree of openness (tree bush cover between 30-40%) and the same substrate (clay on hard fissured limestone), situated at Viols-le-Fort (alt. 240 m) and Causse-de-la-Selle (alt. 245 m).
Comparative data of relative frequencies of numbers (Nb%) and biomass (Bm%) of species trapped over a 12 months period (March 1978 to April 1979).

Species	Viols-le-Fort Nb%	Viols-le-Fort Bm%	Causse-de-la-Selle Nb%	Causse-de-la-Selle Bm%
Trox perlatus	0.11	0.18	0.09	0.11
T. hispidus	0.24	0.19	0.06	0.04
Geotrupes niger	0.32	2.67	0.42	2.51
Scarabaeus laticollis	1.52	15.34	3.16	22.84
S. typhon	0.03	0.55	---	---
Sisyphus schaefferi	5.10	8.62	6.68	8.09
Euoniticellus fulvus	0.13	0.20	---	---
Copris hispanus	0.24	7.19	---	---
Caccobius schreberi	0.72	0.30	0.03	0.01
Euonthophagus amyntas	0.03	0.04	---	---
Onthophagus emarginatus	0.99	0.44	1.36	0.43
O. furcatus	0.19	0.04	0.19	0.03
O. lemur	58.54	45.71	15.49	8.67
O. maki	8.84	5.41	2.29	1.01
O. vacca	0.67	1.60	---	---
O. joannae	8.82	3.18	26.14	6.77
O. coenobita	3.90	4.95	5.10	4.64
O. verticicornis	0.40	0.75	32.78	43.82
O. grossepunctatus	---	---	1.84	0.38
Aphodius erraticus	---	---	0.06	0.02
A. subterraneus	0.03	0.01	---	---
A. haemorrhoidalis	1.55	0.36	0.03	0.005
A. luridus	0.83	0.58	0.61	0.31
A. paracoenosus	0.43	0.06	2.29	0.22
A. pusillus	0.03	0.02	0.03	0.002
A. prodomus	---	---	0.03	0.007
A. biguttatus	0.43	0.02	1.00	0.03
A. quadrimaculatus	---	---	0.03	0.001
A. fimetarius	0.13	0.08	0.09	0.04
A. constans	5.61	1.50	0.16	0.03
A. granarius	0.08	0.02	---	---
Number of species	26		24	
Number of individuals	3 743		3 099	
Total biomass/trap/12 months (mg dry wt)	64 227.6		74 197.8	
Shannon H'o Index of diversity	2.36		2.76	

Garrigue area. Traps have been set up also in the littoral plain under conditions analogous to those of the Camargue.

1. PHENOLOGY IN THE LITTORAL PLAIN

Systematic trapping and dissections of dung beetles were carried out during 1979 to get the relevant data concerning seasonal variations in beetle numbers, flight periods and oviposition at St Nazaire-de-Pézan, a coastal site near Montpellier. Only dung beetles among the Scarabaeinae and the Geotrupini tribe of the Geotrupidae are considered here. Over a 12 months period 11 species from 6 genera were trapped.

Characteristics of the studied site are given in Table 8 and a climadiagram is shown in Fig. 3. Permanent cattle and sheep populations are rare in this area (Lumaret 1978) because sheep are moved from the littoral plain to the plateaux in summer and back before the end of autumn. Cattle are kept inside during winter and the first part of spring, in most places, except the littoral plain. The site was therefore chosen partly on the basis that cattle would be present year round. Table 9 gives the seasonal mean temperatures and annual precipitation (1978/1979) at this site. Mean seasonal and annual temperatures were 54% higher in winter, 22% in summer and 34% annually, when compared with the means for temperate sites located in the mountains, 40 km north.

Beetle activity was monitored using 3 cattle dung baited pitfall traps 50 m apart (Kirk 1983). The traps were set at 0900 and then cleared and reset at 1300 (morning period), 1700 (afternoon period), 1 h before sunset (evening period) and at 0900 the next morning (night period), once a week during the whole of 1979.

Female beetles were examined by dissecting throughout the year to determine the beginning and duration of the oviposition period. The presence of full sized oocytes in the single Scarabaeinae ovariole, or in one of the 12 Geotrupini ovarioles and yellow body (corpus luteum), in the neck of the oviduct, indicated that beetles were parous and currently ovipositing (Tyndale-Biscoe 1978, Kirk 1983).

With the great variation in size between species, total biomass gives another measure of the importance of dung beetle

Table 8

Characteristics of the study site of St-Nazaire-de-Pezan (Hérault).

Altitude (m)	Lat/Long	Mean ann. Ppn. (mm)	Mean ann. Temp (^{o}C).
5	43^{0} 39' N 04^{0} 06' E	682	14.1

Climatic designation (UNESCO/FAO).	Soil structure	pH
Mesomediterranean (attenuated)	50% silt 40% clay 10% sand no stones	7.8

activity (Nealis 1977). Biomass was estimated by weighing 10 specimens of each species after drying for 3 days in an oven at 60°C.

Over a 12 months period a total number of 812 Scarabaeinae and 8 Geotrupini per trap was recorded (Table 10). *Copris hispanus* (L.), *Geotrupes spiniger* Marsh. and *Bubas bubalus* (Ol.) were nocturnal, all other species were diurnal, except *B. bison* (L.) which was nocturnal, but diurnal and nocturnal during autumn (Table 11). The total number of species and % abundance of beetles are shown in Fig. 4.

Numbers were highest in summer (Table 10), but total biomass, because of the presence of the large beetles, *B. bison* and *B. bubalus,* was highest in spring (Table 10). *B. bison* and *G. spiniger* began ovipositing in autumn. *B. bison* was ovipositing until June. All other species began ovipositing in spring and continued until early summer (Table 12). The new generations of all species, with the exception

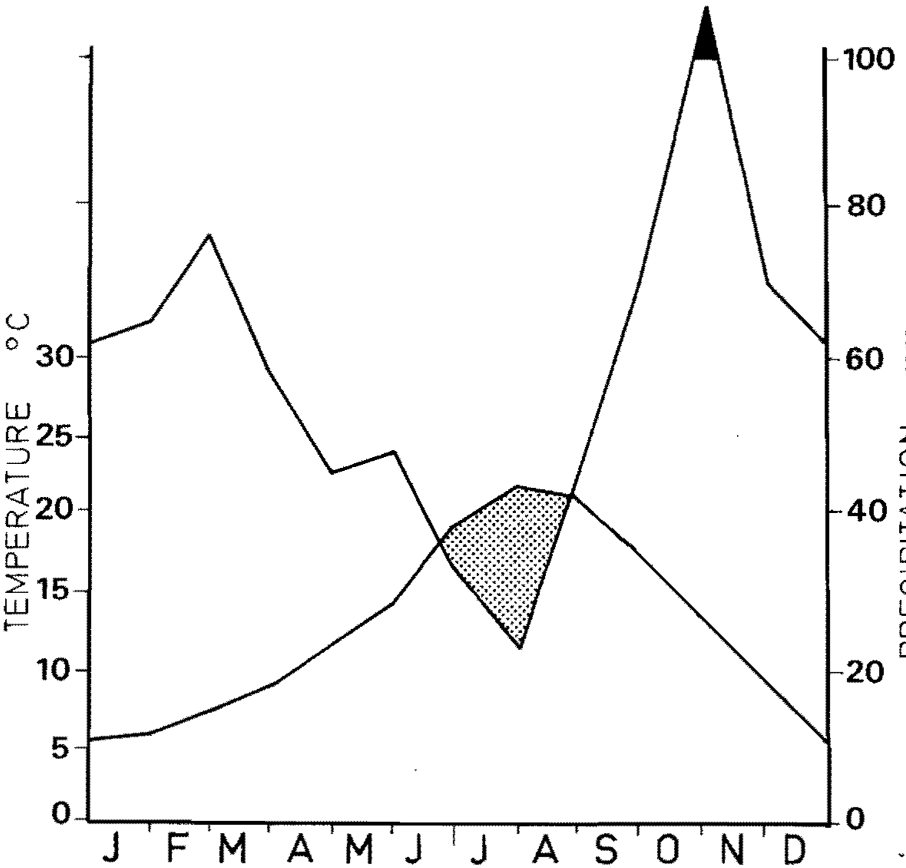

Figure 3

Climadiagram for St-Nazaire-de-Pezan, France (from Walter & Lieth 1960). Precipitation: 682 mm; mean annual temperature: 14.3°C.

Table 9

Mean seasonal temperatures (°C) and seasonal precipitation (mm) at St Nazaire de Pezan (1979) (a poorly drained Camargue type pasture, open and featureless, permanently grazed by cattle).

Season	Mean temperature	Precipitation
Winter	7.8	199.1
Spring	12.2	145.6
Summer	22.1	97.1
Autumn	14.8	234.9
Year	14.2	676.7

of *B. bubalus* and *B. bison*, appeared in the field in summer. *B. bubalus* emerged in spring and *B. bison* in autumn (Table 12).

The cool, moist spring climatic conditions in the mediterranean area are favourable for dung beetle activity. Dung quality (nitrogenous compounds) is also very high in spring (Ricou 1981, Lumaret 1978). Beetle numbers were highest in summer, because of the appearance in the field of the new generations of 5 out of 7 of the most important species (Table 12). Newly emerged females did not oviposit. Dung burial only occurred when females of the species studied here were ovipositing (Table 12). The greatest impact on dung pads therefore occurred during spring when very high percentages of the females of each species were ovipositing (Table 12). Ridsdill-Smith and Kirk (1982) working in Spain, and Paschialidis (pers. comm.) in Attica, Greece, came to similar conclusions about dung beetle activity in those regions.

2. PHENOLOGY IN THE GARRIGUE ZONE

The overall activity of insects searching for food is seasonally variable and depends on the temperature and precipitation

Table 10

Numbers and biomass of dung beetle species trapped/trap in 1979.

SPECIES AND TRIBE	SPRING (MAM) No.	SPRING (MAM) Dry wt	SUMMER (JJA) No.	SUMMER (JJA) Dry wt	AUTUMN (SON) No.	AUTUMN (SON) Dry wt	WINTER (DJF) No.	WINTER (DJF) Dry wt	TOTAL No.	TOTAL Dry wt (mg)
Copris hispanus (L.)	1	513	---	---	1	513	---	---	2	1 026
Euoniticellus fulvus (Goeze)	12	300	74	1 850	10	250	---	---	96	2 400
Bubas bison (L.)	49	10 584	---	---	46	9 936	33	7 128	128	27 648
B. bubalus (Ol.)	45	8 910	6	1 188	---	---	---	---	51	10 098
Onthophagus coenobita (Herbst.)	---	---	3	45	---	---	---	---	3	45
O. ruficapillus Brul.	141	846	245	1 470	14	84	---	---	400	2 400
O. semicornis Panz.	1	10	---	---	---	---	---	---	1	10
O. taurus (Schreb.)	7	224	69	2 208	9	288	---	---	85	2 720
O. vacca (L.)	27	1 107	20	820	---	---	---	---	47	1 927
Caccobius schreberi (L.)	1	7	2	14	---	---	---	---	3	21
Geotrupes spiniger Marsh.	---	---	2	774	4	1 548	2	774	8	3 096
TOTALS No.	283	22 491	418	8 324	84	12 619	35	7 902	820	51 336
%	35	44	51	16	10	25	4	15		

Table 11

Diel flight patterns of dung beetle species at St-Nazaire-de-Pezan (Mediterranean site) (Based on once a week trapping for 12 months (1979); only species trapped more than 10 times used).

Species	Beetle No.	Winter (DJF) % activity				Beetle No.	Spring (MAM) % activity				Beetle No.	Summer (JJA) % activity				Beetle No.	Autumn (SON) % activity			
		Mo	Af	Ev	Ni		Mo	Af	Ev	Ni		Mo	Af	Ev	Ni		Mo	Af	Ev	Ni
O. vacca	0	---	---	---	---	53	48	52	0	0	6	100	0	0	0	0	---	---	---	---
O. taurus	0	---	---	---	---	45	98	2	0	0	38	74	26	0	0	9	100	0	0	0
O. ruficapillus	0	---	---	---	---	377	93	7	0	0	89	92	8	0	0	14	71	0	29	0
E. fulvus	0	---	---	---	---	49	71	29	0	0	84	69	31	0	0	10	50	50	0	0
B. bison	38	0	0	100	0	49	0	0	0	100	0	---	---	---	---	49	0	5	17	78
B. bubalus	0	---	---	---	---	38	0	0	0	100	11	0	0	0	100	0	---	---	---	---

Mo	Morning	09-13
Af	Afternoon	13-17
Ev	Evening	17-1 h before sunset
Ni	Night	1 h before sunset-09

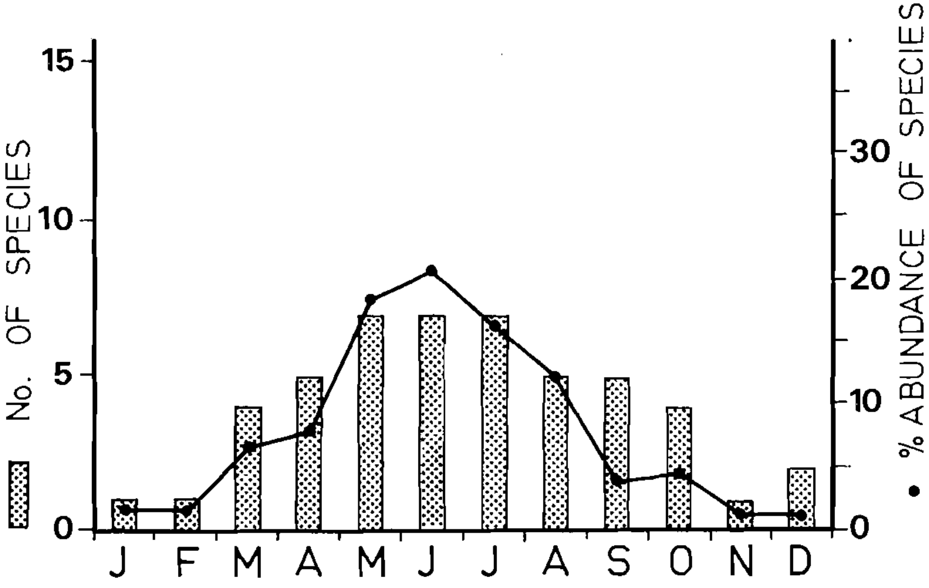

Figure 4

% abundance of species and number of species per month at St-Nazaire-de-Pezan (Camargue site).

cycles. Two activity peaks are normally observed in the Garrigue, a major one at the end of spring and another, much reduced, in autumn (Fig. 5). The first peak, which corresponds to the oviposition periods of most of the species, precedes the summer drought period. The second coincides with the emergence of numerous immature insects, after the first heavy autumnal rains.

In mixed *Quercus ilex* and *Q. pubescens* open Garrigue (locality of Viols-le-Fort, Hérault) the species active in spring represent 61% of the total annual numbers and 56.1% of the total biomass (Table 13). Telecoprids (*Scarabaeus* and *Sisyphus* spp.), still scarce (3.1%), nevertheless constitute 14% of the total of this biomass. *Onthophagus lemur* very largely dominates, both in numbers (73.8%) and biomass (62.7%).

The onset and duration of oviposition, expressed as of the female population with mature oocytes and yellow body present (No species with<5♀ included): emergence of new generation was indicated by presence of females with immature ovaries, no yellow body, with soft cuticles and shiny front tibiae.

	E. fulvus	*B. bison*	*B. bubalus*	*O. ruficapillus*	*O. taurus*	*O. vacca*	*G. spiniger*
% of ♀population with mature oocytes and yellow body							
M	---	100	43	20	---	83	---
A	---	100	77	75	---	100	---
M	100	100	100	92	80	100	---
J	100	---	100	90	83	100	---
J	25	---	100	29	64	14	0
A	0	---	---	9	10	13	0
S	---	5	---	---	0	---	29
O	---	48	---	---	---	---	33
N	---	58	---	---	---	---	---
D	---	59	---	---	---	---	---
J	---	92	---	---	---	---	100
F	---	100	---	---	---	---	---
No. of ♀ dissected	58	307	97	80	121	101	50

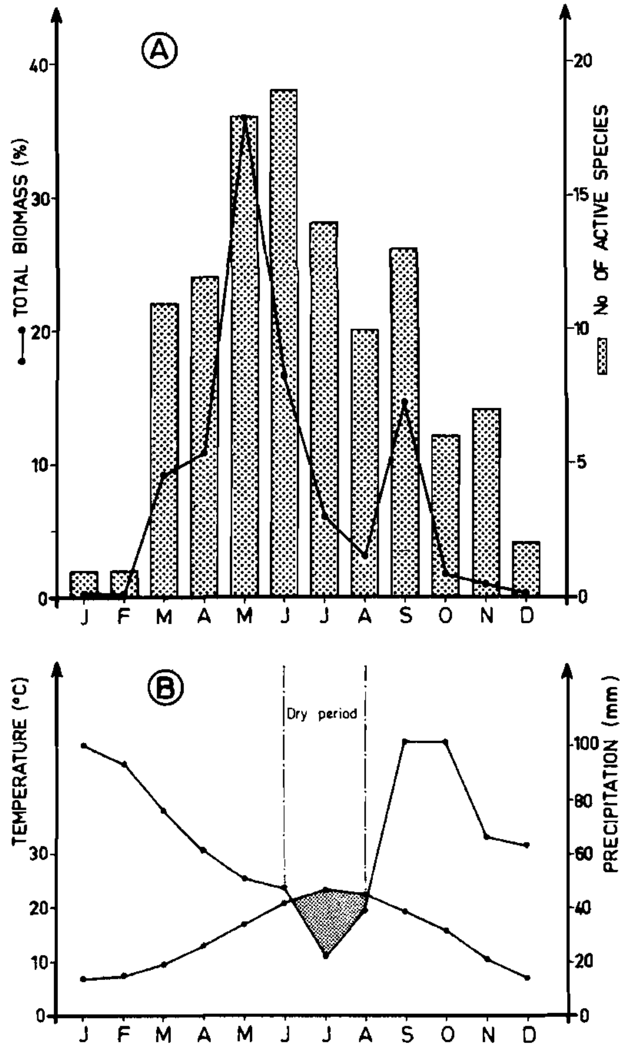

Figure 5

Monthly variation in number of active species and their biomass (% of annual total) at a Garrigue site (Viols-le-Fort, Hérault, France) (A). Climatic diagram for Montpellier - Bel Air (Hérault) (B).

Phenology of insects in an open Garrigue (Viols-le-Fort). Seasonal relative frequencies of species (%) and biomasses (%).

	Winter (D.J.F.)		Spring (M.A.M.)		Summer (J.J.A.)		Autumn (S.O.N.)	
	% Nb	% biomass	% Nb	% biomass	% Nb	% biomass	% Nb	% biomass
Trox perlatus	---	---	.09	.16	---	---	.51	.51
T. hispidus	---	---	.04	.04	.41	.32	1.02	.48
Geotrupes niger	---	---	---	---	.21	1.73	2.55	12.88
Scarabaeus laticollis	---	---	.92	10.08	1.35	13.57	5.87	35.82
S. typhon	---	---	---	---	---	---	.25	3.18
Sisyphus schaefferi	---	---	2.14	3.94	4.77	8.05	24.49	25.07
Euoniticellus fulvus	---	---	---	---	.52	.76	---	---
Copris hispanus	---	---	.22	7.12	.41	12.40	---	---
Caccobius schreberi	---	---	.04	.02	1.76	.73	2.30	.57
Euonthophagus amyntas	---	---	---	---	.10	.16	---	---
Onthophagus emarginatus	---	---	1.23	.59	.73	.32	.51	.14
O. furcatus	---	---	.04	.01	.10	.02	1.28	.17
O. lemur	.97	2.50	73.77	62.67	51.56	40.21	2.04	.97
O. maki	---	---	2.93	1.95	15.87	9.70	28.31	10.50
O. vacca	---	---	.79	2.06	.52	1.24	.51	.74
O. joannae	.97	1.16	5.69	2.24	10.48	3.78	25.00	5.47
O. coenobita	2.91	12.20	4.25	5.87	3.01	3.82	4.34	3.33
O. verticicornis	---	----	.31	.62	.83	1.54	---	---
Aphodius subterraneus	---	---	.04	.02	---	---	---	---
A. haemorrhoidalis	---	---	.22	.06	5.50	1.28	---	---
A. luridus	---	---	1.36	1.04	---	---	---	---
A. paracoenosus	---	---	.57	.08	.31	.04	---	---
A. biguttatus	---	---	.44	.02	.83	.03	---	---
A. fimetarius	---	---	.09	.05	.31	.18	---	---
A. constans	95.15	84.14	4.68	1.33	.41	.11	1.02	.16
A. granarius	---	---	.13	.03	---	---	---	---
Total insects	103		2 284		964		392	
% insects/annual total	2.75		61.02		25.75		10.47	
Total biomass (mg dry weight)	535.8		36 026.9		16 562.3		11 102.6	
% biomass	.08		56.1		25.8		17.3	
Shannon H'o Index of diversity	.30		1.70		2.47		2.68	
Equitability Index	.15		.38		.56		.68	

During the summer the number of insects diminishes considerably due to the drought, even if the number of active species is still high (Fig. 5). The relative importance of *O. lemur* tends to diminish, this species being progressively replaced by *O. maki*.

In autumn the telecoprids largely dominate, both in biomass (64% of the total) and in number of active insects (30.6%). That is due to the emergence of the new generation of *Scarabaeus* and *Sisyphus* (69.2% of *Sisyphus schaefferi* trapped in September are immatures). The autumn emergence, very clear in localities with short vegetation (pastures and open Garrigue, stages n° 1 to 3), is less and less marked as the sites close (stages n° 4 to 6), so that the relative number of active individuals diminishes (Fig. 6).

In general, at any site in the Garrigue only 1 to 3 species represent more than 75% of the total of individuals or their biomass in any given season. They often coexist with numerous other species which always have small numbers, which share the remaining resources available.

Often minor microclimatic differences (of temperature or rainfall) can very markedly modify the periods during the insects are active. For example, at the Viols-le-Fort and Causse-de-la-Selle sites which are very close geographically (Table 7), it is observed that spring emergence of insects is much earlier at Viols-le-Fort which is a slightly warmer site; equally autumn activity continues longer there (Figs. 7 and 8).

V. DUNG UTILIZATION STRATEGIES OF MEDITERRANEAN DUNG BEETLES AND THE RATE OF DUNG DISPERSAL

A wide variety of droppings, each constituting an ecological unit (Mohr 1943) characterized by its own texture, chemical composition, temperature, and humidity, is available to dung beetles. Omnivore mammal droppings, often compact, rich in nitrogenous components and vegetable fibres (wild boar, man), attract a very varied fauna and generally remain attractive long after their complete desiccation. Similar droppings are those of some small carnivores (foxes, genets, etc.) which often contain fur of rabbits or rodents; they attract amongst

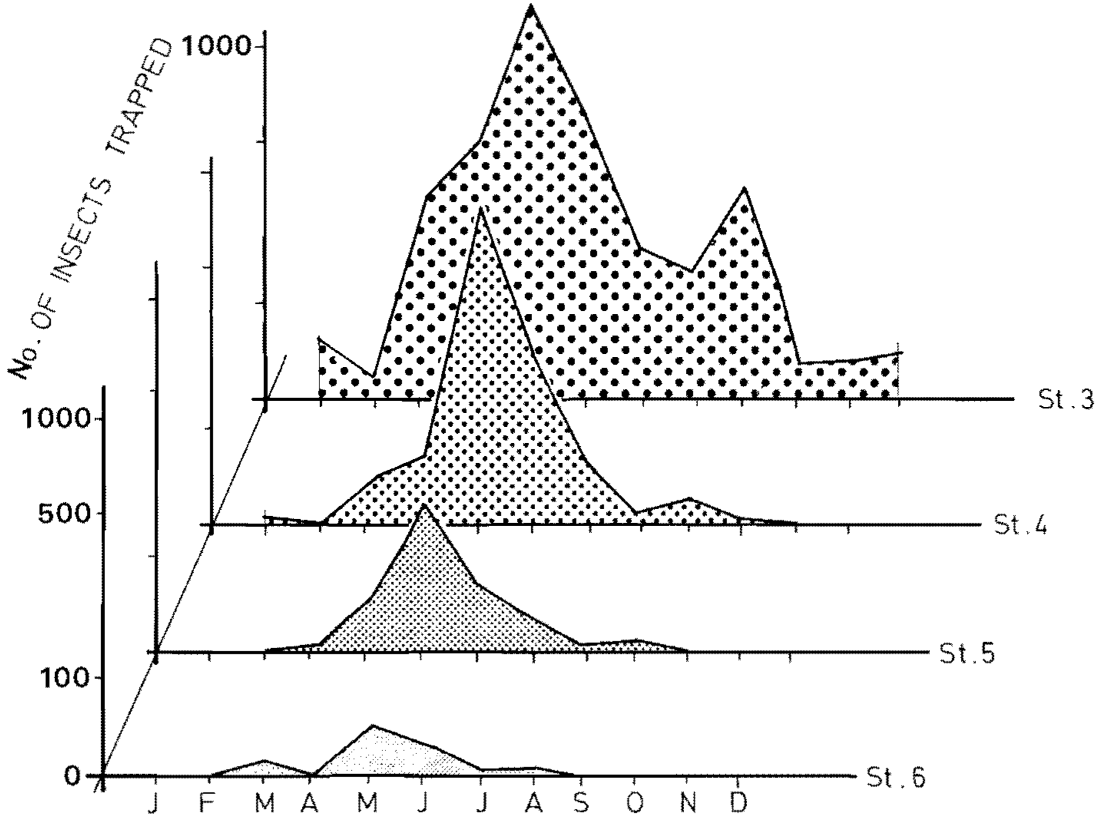

Figure 6

Monthly variations of numbers of insects trapped at 4 Garrigue sites on compact limestone. Habitat gradient from stage 3 (open garrigue) to 6 (forest).

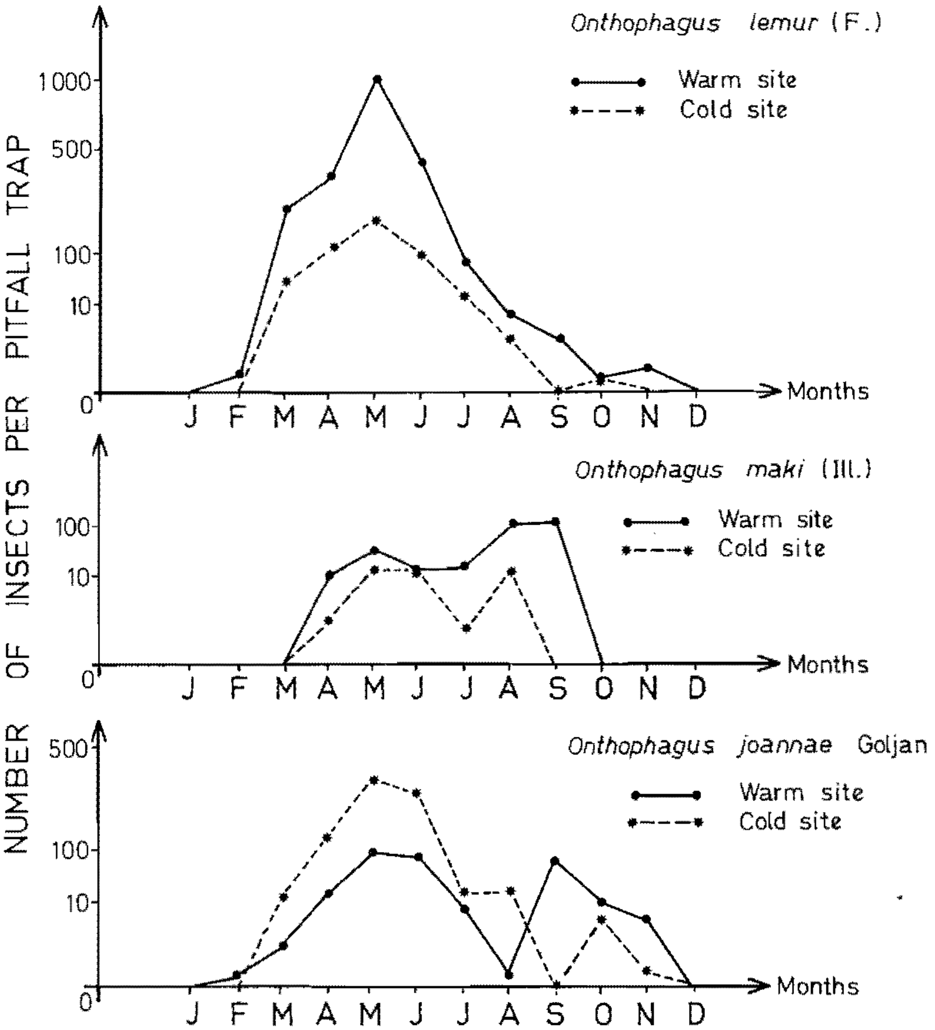

Figure 7

Comparison of the activity periods of *Onthophagus lemur*, *O. maki* and *O. joannae* at Viols-le-Fort (warm garrigue) and Causse-de-la-Selle (cold Garrigue).

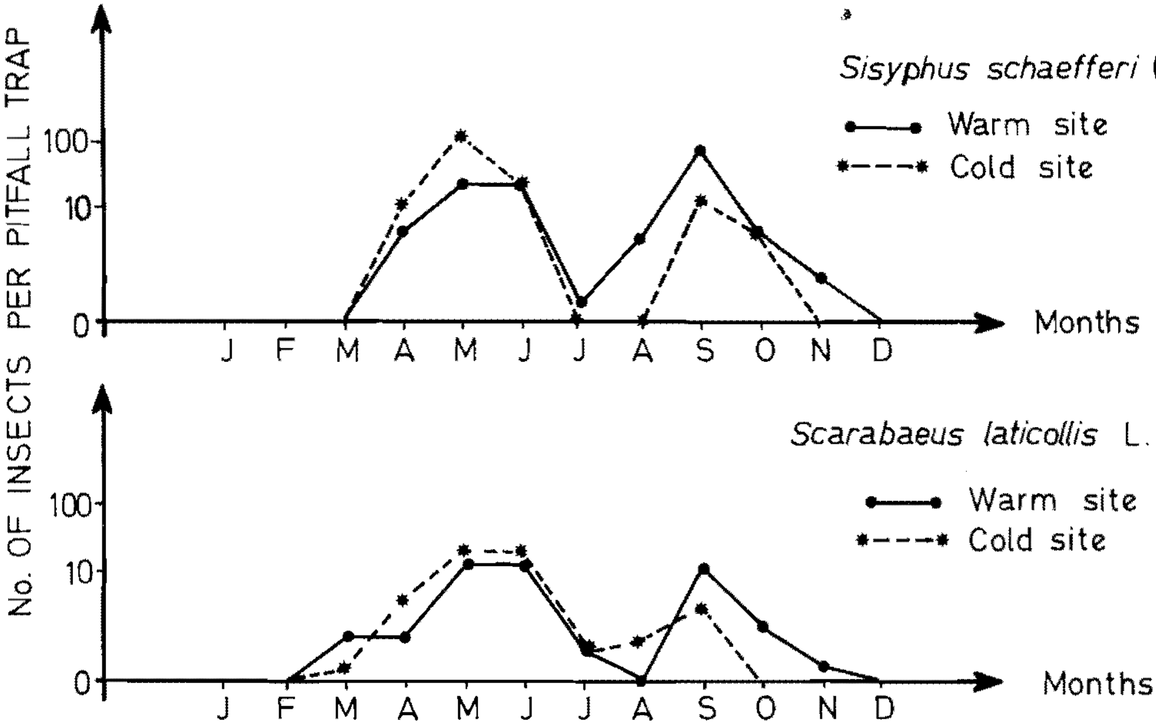

Figure 8

Comparison of the activity periods of *Sisyphus schaefferi* and *Scarabaeus laticollis* at Viols-le-Fort (warm garrigue) and Causse-de-la-Selle (cold garrigue).

others many Scarabaeinae and some Trogidae species (*Trox perlatus* and *T. hispidus*). By contrast, the small pellets of rabbits only attract a tiny part of the dung beetle fauna of a site; these are small species, such as *Onthophagus emarginatus* Muls., *Aphodius elevatus* Ol., or *A. bonnairei* Reitt. which live and reproduce under the faecal mass. The droppings of small rumiants (sheep, goats) are small homogenous pellets and they constiute the main feeding source of dung beetles on the Causses and in the Garrigue. In the Camargue and in the coastal plains, cow pads and horse droppings are the most commonly used.

It is important for most of the dung beetles that droppings be used before their complete desiccation which normally stops the insect colonization process; but sometimes attractiveness can restart partially under some conditions, after wetting of the droppings for example. Taking into account the initial size of dropping, two principal models of faecal maturation can be defined, one represented by cow pads and the other by sheep droppings.

Because of their large size, pads constitute a microbiotope where physico-chemical conditions are evolving during their ageing. They mature relatively quickly under mediterranean climatic conditions, especially in summer, which leads to the differentiation of 3 zones (Lumaret 1975) (Fig. 9): the crust, the intermediate and the deep zones. At the moment of its dropping, the pad is a semi-liquid (about 85% water) and homogenous paste throughout its thickness. Brown or clear-yellow coloured, very compact, it constitutes a strongly reducing environment (Fig. 9, A). Then progressively a crust differentiates, soon becoming dry and brittle. It is separated from the deep zone by an intermediate zone of 60-70% water content, deep brown coloured and well aerated because of the action of numerous insects which form a dense system of tunnels inside (Fig. 9, B). Later, due to its ageing, the crust thickens to the detriment of the intermediate zone which itself thickens, pushing progressively towards the interior of the deep zone which grows thinner (Figures 9, C and 9, D).

This process of maturation is obviously more rapid if the pad is small, insects numerous, and if the weather is hot and dry. In winter, maturation is slower because desiccation is less and the number of active dung beetles is less. Thus, in the Garrigue the complete drying out of a pad dropped in winter requires 2-3 months and sometimes more in the case of the largest pads (20-25 cm in diameter, for a thickness

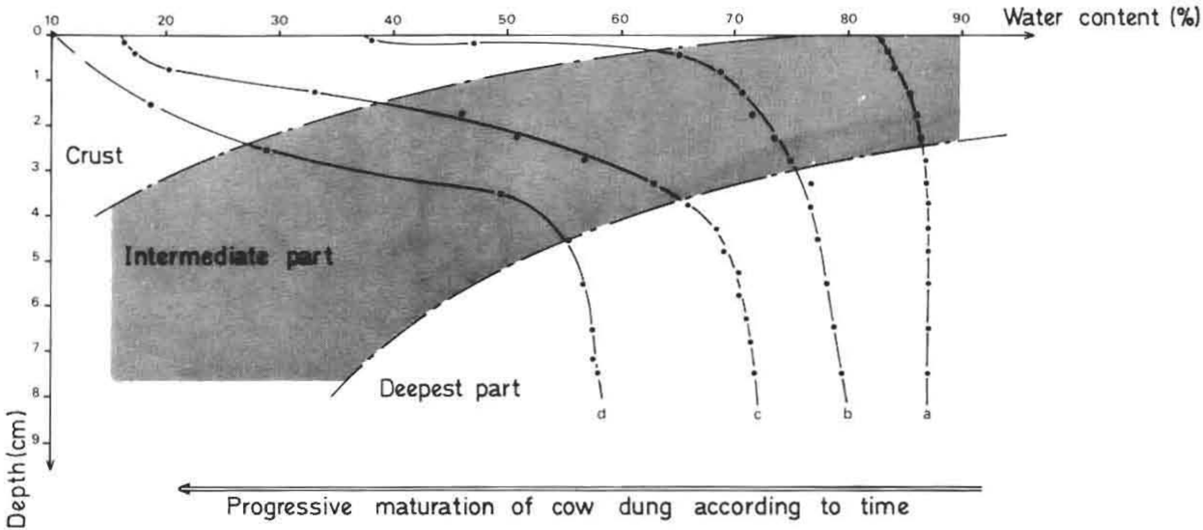

Figure 9

Modifications in water content of a cow pat and the evolution of constituent zones during ageing (carried out in winter in the mediterranean region; in summer dry out is too rapid). Oviposition by *Aphodius* carried out in the intermediate zone. In a 24 hours old pad (a), the crust is non existent; (b) and (c) represent the curves of water content obtained with pads of 3 and 6 weeks old: the delimitation of the intermediate and deep zones is situated at the point of inflexion of the curve. After 10 weeks maturing (d), the thickness of the reducing zone is considerably lessened (from Lumaret 1975).

of 10-15 cm). This allows the larvae of some dung beetles, like *Aphodius constans* Duft. to complete their development inside.

On the contrary, sheep droppings are very different from cow pads. Sheep produce two types of droppings: compact lumps of variable size and weight (from 7.5 to 6 g of dry matter) and single pellets, which may be stuck together (dry weight 0.1 g). There is no significant difference in water content between these two types of droppings when they are produced. However differences very quickly appear, the level of drying out depending on the form of faecal matter produced and the initial mass of the fragments (the surface area/volume ratio being important regarding pellets, lesser for the lumps).

In summer, with soil temperatures of 25°C and 60% atmospheric RH at the moment of dropping (these conditions often being much more severe), the single pellets lose on average 55.4% of their water within only 3 hours; during the same time pellets stuck together (100 g fresh weight) lose 37.2% of their water content whilst the compact lumps lose between 24% for the smallest and 13% for the biggest (Fig. 10). When a sheep pellet has lost more than 50% of its water it attracts almost no more insects. Thus the attractiveness of single pellets is shorter when the weather is hot and dry, which is usually the case from the beginning of summer to the middle of autumn. These single pellets will then quickly dry out. So the piles of stuck pellets and compact lumps, even scarce, are the main feeding source for dung beetles during several months in the Mediterranean area.

The dynamics of the evolution of water content in sheep droppings is in fact a much more complex phenomenon, because over several hours the loss of water becomes a non-linear function of time. If atmospheric humidity conditions are such, a rewetting phase can follow the initial drying out phase. Pellets strongly rehydrate in the case of dew, taking up as much as 50% of the water evaporated off previously; after they may become temporarily attractive again to some dung beetles. In the case of compact lumps, only a pause or even a slowing down in drying out occurs, without a real rewetting phase.

Consequently dung beetles develop different strategies when using cow pads and compact sheep lumps. Cow pads, because of their large volume, can be used in almost all seasons by most of the burying large size species (*Geotrupes, Bubas, Copris*). Herds of cattle are present throughout the year in the Camargue. By contrast

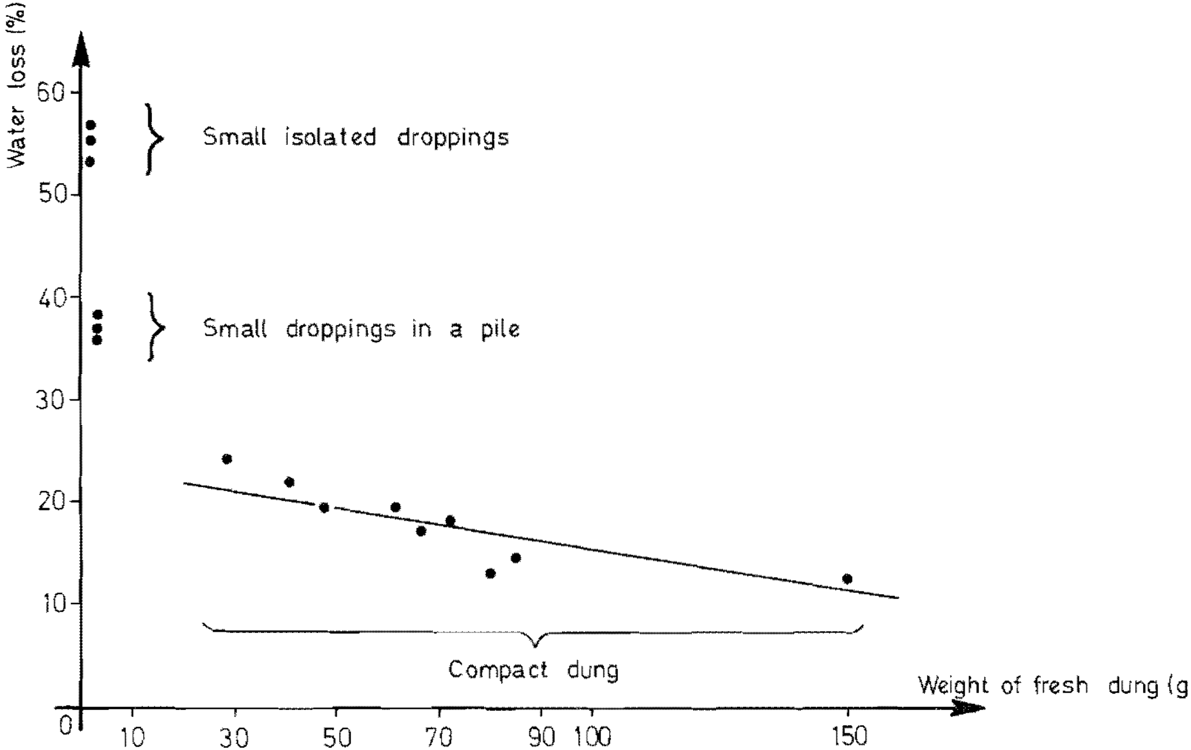

Figure 10

Drying of sheep droppings (% of the loss of free water) following exposure to the air for 3 hours as a function of the initial weight of the dropping.

they are scarce in the Garrigue, being only present there from autumn to early spring.

In the Garrigue only some winter active species are able to exploit cow pads. This is the case for *Aphodius constans,* its oviposition generally starting at the beginning of February, sometimes earlier, if conditions are favourable; it goes on until April. Large numbers of adults (up to 100/pad) are found inside each level of the pads, from the crust to the deeper zone. Eggs however are laid only in the intermediate zone, between very narrow limits of humidity (55-75%) with an optimum of about 68%. Depending on the ageing of the pad, the intermediate zone shifts towards the bottom, which leads females to oviposit deeper to follow the displacement of the optimal zone (Lumaret 1975). The eggs laid near the surface are therefore the oldest. Larvae as soon as they emerge burrow progressively deeper and deeper into the pad to avoid the desiccation front represented by the thickening of the crust (Fig. 9). These larvae end up by joining in the lower levels the latest hatched larvae and the most recently laid eggs, and they compete with them. So young larvae are often eliminated by the oldest larvae which colonize the whole dung pad (average density: 1 larva/4 cm^3). This tends towards an uniformly aged larval population. When they are 6-8 weeks old, depending on the temperature, larvae reach the 3rd instar stage. Then they migrate into the soil and pupate there. Such a strategy in the use of dung for breeding can only be developped because droppings remain usable over a long period. The initial size of the dung when dropped is the most determinant factor.

Cattle dung burial by Scarabaeid beetles was studied also at a typical Camargue pasture (Bassett 1978), at 5 m altitude in a mediterranean climatic area (mesomediterranean, UNESCO-FAO, 1963), near Montpellier, France, during 1979-1980. The Onitini *Bubas bison, B. bubalus* and the Onthophagini *Onthophagus vacca* were the most important dung beetle species present. These species only buried dung when females were ovipositing (Kirk unpublished data). *B. bison* actively buried dung from September to June and *B. bubalus* and *O. vacca* from March to July (Kirk 1983). Female beetles were dissected and those with full sized oocytes and signs of corpus luteum (yellow body) in the oviduct were considered to be parous and actively ovipositing (Tyndale-Biscoe 1978). Fig. 11 shows the soil temperature at 10 cm depth and the build up in numbers of parous females of *B. bison, B.*

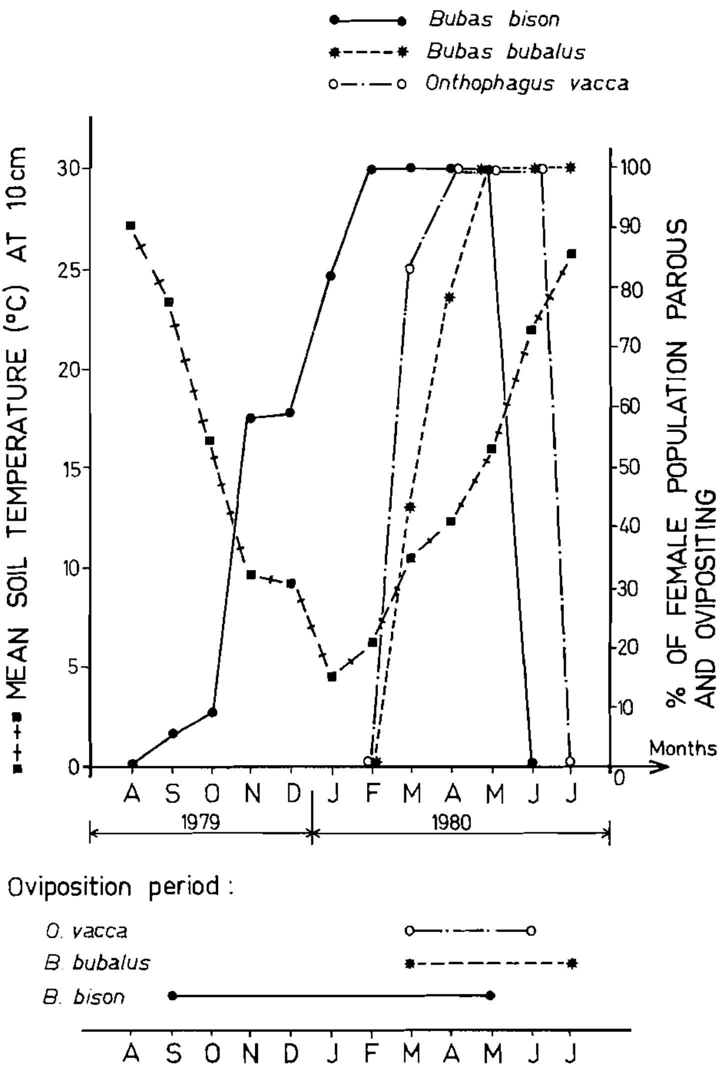

Figure 11

Percentage of females of *Bubas bison, Bubas bubalus* and *Onthophagus vacca* parous and ovipositing (burying dung).

bubalus and *O. vacca* and consequently of dung burial. *B. bison* females oviposited at a rate of 0.5 eggs/day in September, October, March and April but only 0.03 eggs/day in January. Low temperatures in winter slowed down oviposition and therefore dung dispersal by *B. bison.* Both *B. bison* and *B. bubalus* buried an average of 67% (197 g dry weight) of a cattle dung pad (279 g mean dry wt.) at the height of their activity periods in autumn and spring (Kirk 1983). The dung was buried in tunnels 150-230 mm in length, each dung mass weighing on average 10.5 g dry wt. and being 96 mm long. The unburied portion of the pad was partly consumed by the beetles and other organisms and the rest rapidly disintegrated by the action of the weather. *O. vacca* tunnels were 50-100 mm in the length and filled with 10-15 mm of dung, each mass weighing on average 0.9 g dry wt. During the spring months April-June, when the 3 species were active, cattle dung pads were completely dispersed in 15-28 days. The same rate of dispersal was recorded in October, slowing down in November and over the winter months. However, dung dispersal occurred in every month from September to July.

The strategies of utilization of dung and the reproductive strategies related to them are different regarding sheep droppings. The type of dropping represents a transient source of food, which dries within several hours or days. Consequently the insects have developped diverse behaviour, tending to remove this material as quickly as possible from other consumers and the unfavourable action of the habitat. From the beginning of spring until the arrival of the summer drought (June to July, depending on the year), the soil is relatively humid and therefore soft enough to allow numerous species to dig tunnels for oviposition. If the strategy of paracoprids (*Onthophagus, Copris, Bubas*) and telecoprids (*Scarabaeus, Sisyphus*) is relatively well known and does not differ fundamentally from that observed in other climates, the conditions under which such a resource is utilized by the *Aphodius* spp. in a mediterranean climate are less well known.

Most of the *Aphodius* ovipositing in spring or summer do not deposit their eggs directly into the lumps of sheep droppings because these do not allow the complete development of larvae before they completely dry out. *A. (Acrossus) luridus* F. oviposits, for example, at the soil/dropping interface. The eggs, extremely resistant to drought, give rise to larvae which immediately dig a narrow tube like burrow into the still humid soil directly under the dropping. This is then filled with dung by the larva itself, which adds to its reserves each time the dropping is rewetted by rain or dew. *Aphodius erraticus* develops a similar strategy to that observed by Rojewski (1983). In that case however the female digs a true branched nest and stocks dung by herself inside for the larvae. This nest looks very similar to the *Geotrupes's* nests, as eggs are laid inside small individual cells above the feeding part.

During summer, drought stops nearly all dung beetle activity. Insects cannot easily dig the soil because of its hardness. Feeding resource are scarce because a large part of the sheep flocks leave the region for better pastures higher up (transhumance).

The sheep which remain have only a short dry pasture and produce only dry pellets, unattractive to beetles. Thus between the end of spring and the beginning of autumn those droppings not immediately used accumulate in the pastures. The September rains rewet this material which has been dried out for several months and which is then exploited by tiny *Onthophagus* spp. such as *O. emarginatus* Muls., which utilize the smallest pellets (0.1 g dry wt) and by several *Aphodius* spp. such as *A. (Ammoecius) elevatus* Ol., consuming the largest droppings (>10 g dry wt).

After every shower *O. emarginatus* digs a tunnel directly under the pellets, throwing out all the soil around and underneath; thus the pellets progressively sink (3-5 cm deep) and stick to the sides of the tunnel, allowing their complete utilization. These beetles behave in this way until winter and begin again as early as the following spring.

The strategy adopted by *A. elevatus* is different as it uses the large compact sheep droppings. In autumn and at the beginning of winter *A. elevatus* oviposits several eggs into each dropping which do not hatch until the wetting level of the dropping is sufficient. The larvae live inside the dropping during their development, which lasts 2-3 months, pupation following later in the soil. This type of development may be compared to that of *A. constans,* but the 2 species are not competitors because they do not exploit the same types of resource (cow pad and sheep droppings respectively), even though they cohabit in the same biotopes.

Consequently it is the compact sheep lumps dropped in the Garrigue at the beginning of spring (April) which disappear quickest from the soil surface. Nearly 50% of their mass is used within the first month, and only 27% for the single pellets; nevertheless 8 months after, most of the droppings have disappeared (Ricou 1984). The droppings produced in summer disappear less quickly due to the drought, and despite their earlier exploitation, 70% of the lumps and 50% of those of pellets only are utilized after 8 months. Of those droppings left in winter (December), 30% of their dry matter still remains on the ground after one year, this proportion reaching 60% in the case of pellets.

The situation is similar even on the Causses which benefit from a mediterraneo-mountain climate, often with dew during summer. A simple shifting in timing of the sheep droppings rate is observed, spring being later than in the Garrigue due to the altitude (800-1000 m). The droppings produced in May-June have dissapeared most rapidly due to the high number of active species. After one month, 84.6% of lumps have disappeared, but only 37.9% of pellet piles and 5.4% of single pellets. Starting in August until September-October, the rate of used droppings very strongly diminishes, 10.7% only of the lumps being utilized after one month. Droppings produced during the November-April period disappear within 6-8 months, but in that case earthworms and detritus feeding Myriapoda complete the action of the dung beetles.

VI. DISCUSSION

Despite its apparent homogeneity the French mediterranean region is made up of numerous contrasts. The mosaic-like distribution of countryside, the structure of vegetation cover and the differences in nature of the geological substrate have had considerable effects on the structure of dung beetle communities.

Diurnal insects are in the great majority and divide up the trophic resources of the habitat in a relatively equal manner, the substitutions which operate throughout the year in each guild allowing a reduction in competition between the dominant species.

Despite the very similar trophic needs of the 4 *Onthophagus* spp. which dominate in *Brachypodium ramosum* pasture (Table 4), *O. lemur* (41.7% of the total annual trapped number), *O. vacca* (23.9%), *O. maki* (5.5%) and *O. emarginatus* (5.8%), competition between them remains low. The coexistence of similar sized populations of *O. lemur* and *O. vacca* in the same biotopes is due to a slight difference in their activity rhythm during the day, a much larger shift in the starting times of their reproductive periods (Fig. 12) and the exploitation of differ-

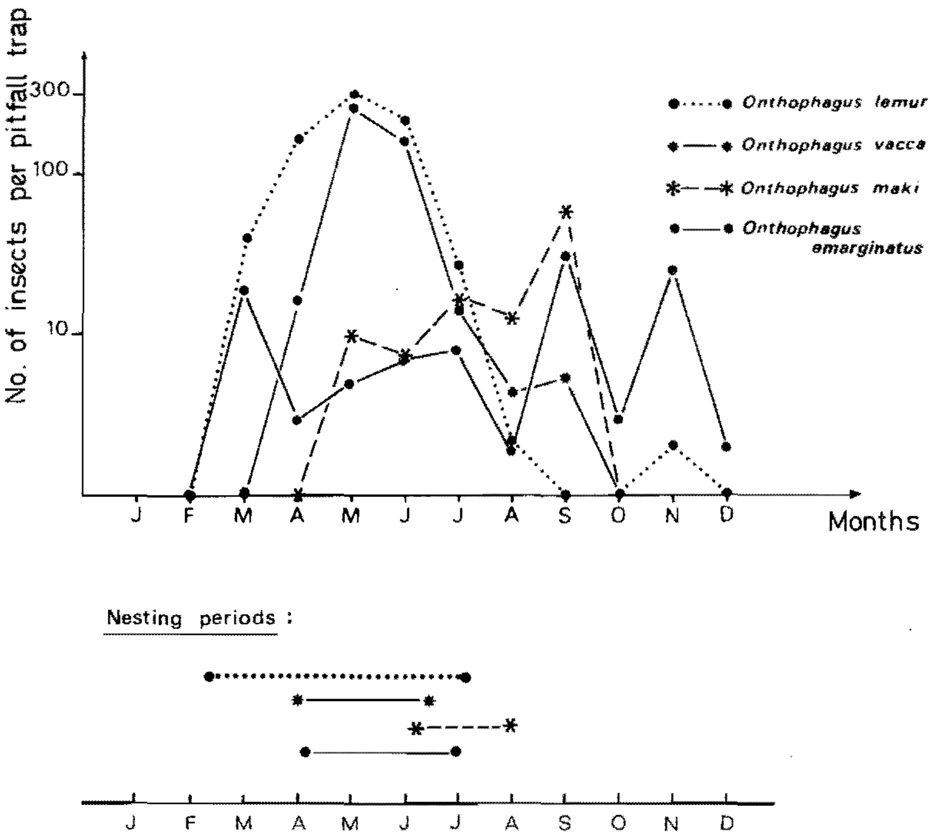

Figure 12

Monthly evolution of *Onthophagus* trapped in Garrigue and breeding periods corresponding to those species.

ent levels of soil situated directly under the dropping, the rearing tunnels for *O. lemur* larvae being shallower than those of *O. vacca* (Fig. 13).

By contrast, the biological differences between *O. lemur* and *O. maki* are slight. However, the coexistence of these 2 species at the same site is possible because of a difference in their reproductive and emergence periods. Oviposition by *O. lemur* starts at the end of April and continues until June, *O. maki* only appearing in May, its oviposition period taking place between the end of May and August, which strongly reduces competition between them for additional dung to stock brood tunnels (Fig. 12).

O. emarginatus exploits dry, often old, small droppings, and its activity can continue without problems during the whole year. The fact that *O. emarginatus* digs a very shallow tunnel gives it the possibility of forming brood tunnels under a dropping containing the previous species, by exploiting a soil level free from competition.

The succession of species in time and their replacement by others utilizing the resources of the habitat, in the same way, means that the observed guilds can be considered as relatively stable and functional groups, several species being able to play the same role. From one site to another the dominant species can change (Table 7) without greatly modifying the functioning of the system. Likewise the indexes of diversity of these sites are very close.

Differences appear in a comparison of the seasonal patterns of adult dung beetle activity between Southern France (present work) and South-Western Australia (Ridsdill-Smith and Hall 1984, Ridsdill-Smith and Lumaret unpubl.). In Australia endemic insects are active even in winter while, in the French garrigues, very few are active during this season (Table 9). Differences in winter temperatures between the two situations may explain these divergent results. However, several species from Southern France (particularly *Copris hispanus* and *Bubas bison*) have been proposed for introduction to S.W. Australia in an attempt to achieve biological control of bush fly (*Musca vetustissima* Walker) (Ridsdill-Smith and Kirk 1985).

Because of a high number of species in most of the French mediterranean dung beetle communities, the level of interspecific competition seems to be low. We agree with Hanski's idea (1986) that, because intraspecific beetles fly away from a group of pads or to another pasture, then that part of the resource that remains unutilized

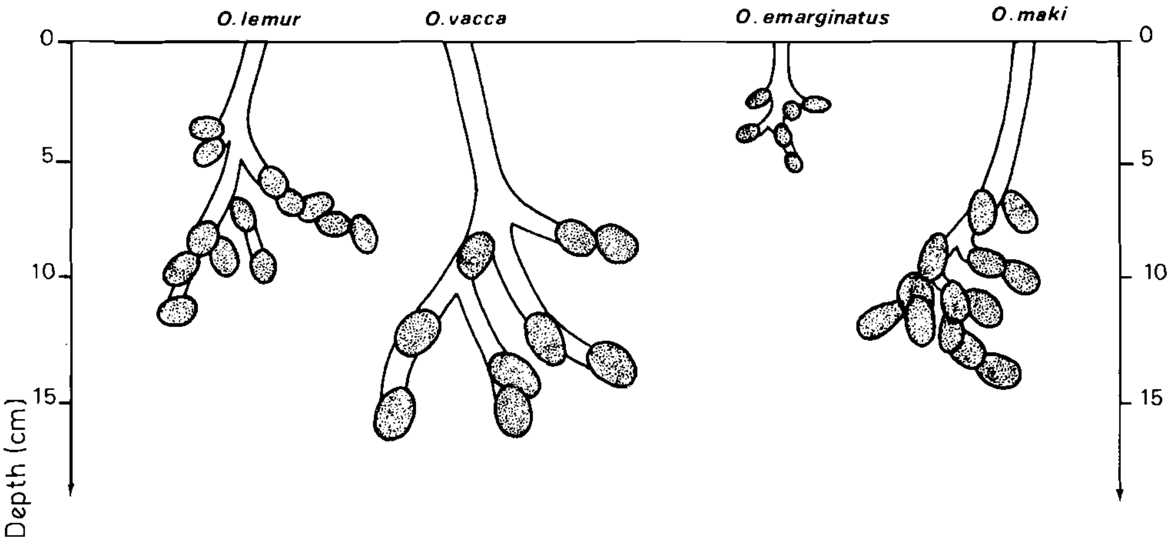

Figure 13

Form and depth of tunnels of *Onthophagus lemur, O. vacca, O. maki* and *O. emarginatus.*

by one species can be partly used by another one and so on, making coexistence possible. Diversity in guilds and in behaviour contributes to maintaining a low level of remnant dung on the soil surface, and thereby a low level of cattle parasites (flies and helminths).

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