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Il popolamento delle Alpi Occidentali

Biogeography of dung beetle communities in the western and central Alps (Coleoptera, Scarabaeoidea)

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SUMMARY

Geographic origin and diversity of the dung beetle fauna was studied in two Alpine regions, namely the Vanoise National Park (France) and the Swiss National Park (Grisons) which showed thirty and twenty nine species respectively, with twenty-two species being common. Organisation and dynamics of the dung beetle communities were analysed in upper Maurienne Valley (Vanoise NP and peripheric area). The richness of the fauna was related to the range of climatic conditions and to abundance as well as diversity of the large mammal fauna living there throughout the year. The diversity index decreases as the altitude increases, and the equitability index varies in the same way. All the species assemblages are log-linear types and may be fitted to Motomura's model. Several core species develop during the favourable period. In subalpine communities, four successive waves of species replace each other from spring to autumn, whereas, in the highest sites, communities are dominated by a single species which extends its activity throughout the favourable period.

1. INTRODUCTION

Mountains are characterized by high rates of insolation and radiation, reduced atmospheric pressure, great diurnal fluctuations in temperature, and low average temperature leading to snow precipitation. Atmospheric aridity increases with elevation because water vapour tension is reduced. Dung beetles, which constitute an ecological group of insects whose specific richness and community assemblages influence the functioning of pastures, have to respond to these constraints. Their successive swarming facilitate a rapid use of almost all faeces.

Many dung beetle species have been collected in high mountains all over the world, up to 5000 metres in Tibet and the Himalayas (Mani & Singh, 1961; Mani, 1968; Stebnicka, 1986, 1989, 1990). Biogeographical data on montane dung beetles, including their altitudinal distributions, have been compiled and discussed by Horion (1950) for the Alps and the Carpathians, and Lumaret and Stiernet (1989, 1991) for the Western and Central Alps. The altitudinal limits of the species above the timber line show many striking differences, depending on the massiveness of the trend lines of the mountain ranges, the topographical peculiarities and chiefly the latitude which controls the climatic conditions and the length of the active period (Lumaret and Stiernet, 1991).

2. ORIGIN OF FAUNA

The present work is focussed on the study of dung beetle ecology and biogeography in the French and Swiss Alps because recent investigations have been carried out mainly in the French National Park of Vanoise and in the Grisons National (Lumaret & Stiernet, 1989; Stiernet & Lumaret, 1991).

The Vanoise NP (528 km^2) lies at altitudes ranging from 1250 to 3852 m. The relief is broken, with 107 peaks exceeding 3000 m. Forty-five per cent of the area belongs to the mats and meadows zone of vegetation, extending from the lowest limit of snow patches in July to the upper limit of animal life. Human influence is low, except during summer, when sheep and cattle from adjacent valleys are grazed in the subalpine and alpine meadows up to 3000 m. The park has a rich fauna of wild mammals, including wild goats, chamois, marmots and hares.

The Grisons NP is smaller (170 km^2) and stretches between 1700 and 3164 m in altitude. Wild mammals are numerous: red-deers, chamois, wild goats, roe-deers. In addition, the occurrence of cattle, sheep and of a few horses, all outside the park limits, increases the abundance and diversity of dung in the Grisons district.

France and Switzerland differ in dung beetle richness: 149 species in France (Lumaret, 1990) versus 92 species in Switzerland. These countries have 87 species in common which represent 58% of the French fauna and 95% of the Swiss fauna respectively (Tab. I). Aphodiidae are dominant in Switzerland (69.6%, versus 61.7% in France). Conversely Scarabaeidae are more important in France than in Switzerland (28.9% and 19.6% respectively). Such results are not surprising, as *Aphodius* are the dominant dung beetles in the north temperate region and in montane regions. These differences depend, at the same time, on climatic, edaphic and elevational constraints, on differences in surface of the countries and on the geographical origin of the species. For example, the genus *Thorectes*, widely distributed in Spain and in North Africa, is absent in Switzerland (4 species in France). In the same way, the genera *Scarabaeus* (5 species in France), *Onitis* and *Bubas* are absent in Switzerland. From the opposite point of view, several Eurasian and Eastern-alpine species (e.g. *Aphodius serotinus, A. limbolarius, Onthophagus gibbulus*) do not extend out of Switzerland towards the West.

The geographical distribution of montane dung beetles depends, like that of an insular fauna, on the present structure and the past history of their discontinuous environment. Several examples of dung beetle distributions from various parts of the world indicate that mountains constitute both differentiation centres and refuges. A striking example are the occurrence of the two true alpine subgenera of *Aphodius*, namely *Agolius* and *Neagolius*, along the whole of the alpine arc, from Spain to the Himalayas (subgenus *Agolius*) and from Spain to Central Asia (subgenus *Neagolius*) (Tab. II). Most species and subspecies are endemics and are patchily distributed in restricted mountain areas. All these species reach high altitudes, rarely occurring below 1800

Table I - Comparison between French and Swiss dung beetle fauna.

TAXA	FRANCE	SWITZERLAND	TOTAL SPECIES	COMMON SPECIES FRANCE/SWITZERLAND
GEOTRUPIDAE	14	10	16	10
Odontaeus	1	1		1
Typhaeus	1	1		1
Geotrupes	4	4		4
Anoplotrupes	1	1		1
Trypocopris	3	3		3
Thorectes	4	0		0
APHODIIDAE	92	64	96	60
Aphodius	87	59		55
Euheptaulacus	3	3		3
Heptaulacus	1	1		1
Oxyomus	1	1		1
SCARABAEIDAE	43	18	44	17
Scarabaeini	5	0		0
Gymnopleurini	4	1		1
Sisyphini	1	1		1
Coprini	3	1		1
Onitini	5	0		0
Oniticellini	2	1		1
Onthophagini	23	14		13
TOTAL	149	92	156	87

m. Most of them are saprophagous, and only a few of them (several *Agolius* species) are attracted by dung. Sexual dimorphism is often so marked that some females were first described as a distinct species (Dellacasa, 1983). An examination of morphological characters leads to the conclusion that the *Agolius* and *Neagolius* subgenera are relicts with few affinities with other *Aphodius* (Baraud, 1977).

In order to eliminate most of the differences which are not mainly due to montane constraints, only the species from the Vanoise and Grisons regions reaching up to 1600 m elevation (subalpine and alpine levels) will be considered here. Only 30 species occur in the Vanoise NP at such altitudes: 23 Aphodiidae (genera *Aphodius* and *Euheptaulacus*), 4 Scarabaeidae (genus *Onthophagus*), 3 Geotrupidae (genera *Geotrupes, Anoplotrupes, Trypocopris*). In the Grisons NP, the ratio is quite similar: 29 species in total, 24 Aphodiidae, 1 Scarabaeidae and 4 Geotrupidae respectively (Tab. III). The two areas have 22 species in common, 18 Aphodiidae (64% of total > 1600 m), 1 Scarabaeidae (25% of total) and 3 Geotrupidae respectively (75% of total).

Faunistic differences between Vanoise NP and Grisons NP mainly concern Aphodiidae and Scarabaeidae and can be explained both by ecological factors (nonmontane species found up to 1600 m on exposed slopes) (Luma-

Table II - Geographic differentiation in *Agolius* and *Neagolius* subgenera (data from Balthasar, 1964; Stebnicka, 1975; Baraud, 1977; Paulian and Baraud, 1982; Dellacasa, 1983).

Species	Distribution
Subgenus Agolius (Muls. & Rey)	
Aphodius abdominalis	Western Europe, from Spain to Austria
ssp. pecoudi	Cordillera Cantabrica (Spain) ; Pyrenees
ssp. balazuci	Massif Central (France)
ssp. abdominalis	French Alps ; Switzerland ; Austria ; Appenines ; Carpathians
ssp. emilianus	Appenino Emiliano (Italy)
A. bonvouloiri	Central Spain
ssp. cantabricus	Cordillera Cantabrica (Picos de Europa, Spain)
Subgenus Neagolius W. Kosh.	
A. abchasicus	Armenia ; Caucasus
A. amblyodon	Western Alps : Mont Cenis (France) and Valle Stura (Italy)
A. falcispinis	Turkestan ; Mongolia
A. haroldi	Turkestan ; Himalayas
A. heydeni	Portugal ; Asturias (Spain) ; Pyrenees
A. liguricus	South of French Alps ; Liguria (Italy)
A. limbolarius	Switzerland ; Austria ; Dolomites ; Albania
ssp. danielorum	Switzerland ; Austria (West Tyrol) ; North Italy (Alpi Retiche, Alpi Orobie, Prealpi Bresciane)
A. montanus	From Pyrenees to Western Alps ; Dolomites ; Yugoslavia ; Bulgaria ; Caucasus
A. montivagus	Southeastern Austria
ssp. cenisius	Mont Cenis (Western Alps, France)
A. penninus	Northwestern Italy (Alpi Pennine)
A. pollicatus	Northwestern Italy (Prealpi Venete ; Julian Alps)
A. praecox	Southwestern Austria
A. roniticus	Tadzhikistan (USSR)
A. schlumbergeri	Western Europe, from Spain to Italy :
ssp. temperei	Western Pyrenees
ssp. schlumbergeri	Pyrenees
ssp. consobrinus	North Italy (Alpi Orobie, Prealpi Lombarde, Prealpi Venete) ; Alpi Apuane (isolated population)
ssp. samniticus	Central Italy (Abruzzi, Basilicata)

ret & Stiernet, 1989, 1991) and by the species chorology (endemism or distribution limited towards East or West). Chorological differences concern 7 species: *A. abdominalis* (euro-alpine species), *A. amblyodon* and *O. baraudi* (alpine (s.str.) species), *A. limbolarius* (Eastern-alpine species) and *A. satyrus, A. pyrenaeus, T. alpinus* (Western-alpine species). All the other species have wider distributions (Tab. III).

3. THE ALPINE DUNG BEETLE COMMUNITIES

During the 1985-1987 period, the seasonal dynamics of dung beetle communities has been studied in the upper Maurienne Valley (Vanoise NP).

Table III - World distribution of dung beetles recorded in the Vanoise National Park (VNP), in the Swiss National Park (SNP) and in the Grisons district (GR).
Vertical line corresponds to the 1600 m level. Each * corresponds to a 200 m step. Chorology according to La Greca's (1964) nomenclature.

	DISTRIBUTION	VANOISE	SWITZERLAND	ALTITUDE <1600m	ALTITUDE >1600m
APHODIIDAE					
Aphodius erraticus (L.)	Eurasia and Maghreb	VNP	SNP	* *	* * * * * *
Aphodius fossor (L.)	Eurasian	VNP	SNP	* *	* * * *
Aphodius haemorrhoidalis (L.)	Eurasia and Maghreb	VNP	SNP	* *	* * * * * * *
Aphodius brevis Er.	Eurasian		SNP	* *	
Aphodius putridus (Fourc.)	Mid-Euro-Turanian	VNP		*	* * * *
Aphodius luridus (Fab.)	Eurosiberia and Maghreb	VNP	SNP	* *	
Aphodius depressus Kug.)	Eurasian	VNP	SNP	* *	* * * * * *
Aphodius rufipes (L.)	Eurasia and Maghreb	VNP	SNP	* *	* * * * *
Aphodius abdominalis Bon.	Euro-Alpine	VNP	SNP	* *	* * * * * * *
Aphodius limbolarius Reit.	East-Alpine		SPN	*	* * *
Aphodius amblyodon Dan.	Alpine (s.str.)	VNP			* * *
Aphodius sticticus Panz.	Euro-Anatolico-Caucasian	VNP	GR	* *	
Aphodius distinctus (O.F. Müll.)	Euro-Turanian		SPN	*	
Aphodius prodromus (Brahm)	Eurasian		SPN		* * *
Aphodius sphacelatus (Panz.)	Euro-Anatolico-Caucasian and Maghreb		SPN		* * *
Aphodius serotinus Panz.	East-Eurasian		SPN	*	*
Aphodius obscurus (Fab.)	South-centro-Euro-Anatolico-Caucasian	VNP	SPN	* *	* * * * * * *
Aphodius immaturus (Muls.)	West-Alpine	VNP		*	* * * * * * *
Aphodius merdarius (Fab.)	Euro-Turanian		SPN	* *	
Aphodius pusillus (Hbst.)	Eurasian	VNP	SPN	* *	* * * *
Aphodius coenosus (Panz.)	Euro-Turanian		SPN	*	* *
Aphodius fimetarius (L.)	Mediterraneo-Eurasian	VNP	SPN	* *	* * * * * *
Aphodius foetens Fab.	Eurasian	VNP	SPN	* *	* * * * *
Aphodius satyrus Reitt.	West-Alpine	VNP	SPN	*	* * * * * * *
Aphodius piceus Gyll.	Boreo-Alpine		SPN	* *	* * * * *
Aphodius pyrenaeus Jacq.Duv.	West-Alpine	VNP			* * *
Aphodius ater (De Geer)	Eurasia and Maghreb	VNP	SPN	* *	* * * * * *
Aphodius constans Duft.	South-centro-Euro-Anatolico-Caucasian		SPN	* *	*
Aphodius uliginosus Hardy	Eurasian	VNP	SPN	*	* * * * * *
Aphodius sordidus (Fab.)	Eurasian		SPN	*	
Aphodius rufus (Moll)	Eurosiberian	VNP	SPN	* *	* * * *
Aphodius alpinus (Scop.)	Mid-European	VNP	SPN	* *	* * * * * * *
Aphodius corvinus Erich.	Mid-European	VNP	SPN	* *	* * * * *
Aphodius granarius (L.)	Cosmopolitan	VNP	SPN	* *	* * * *
Euheptalaucus carinatus (Germ.)	South-Centro-Eurasian	VNP		*	* * * * * *
Euheptalaucus villosus (Gyll.)	North-Centro-European	VNP	SPN	*	* * *
Oxyomus silvestris (Scop.)	Eurasia and Maghreb	VNP	GR	*	
SCARABAEIDAE					
Euoniticellus fulvus (Goeze)	South-centro-Euro-Mediterraneo-centro-Asian	VNP	GR	* *	
Onthophagus taurus (Schreb.)	South-centro-Euro-Turanian and Maghreb	VNP	GR	*	
Onthophagus verticicornis (Laich.)	South-centro-Euro-Turanian	VNP	SPN	*	
Onthophagus ovatus (L.)	South-centro-Euro-Anatolico-Caucasian	VNP	SPN	* *	
Onthophagus joannae Goljan	South-centro-European	VNP		* *	*
Onthophagus baraudi Nic.	Alpine (s.str.)	VNP		* *	* * * *
Onthophagus coenobita (Hbst.)	South-centro-Euro-Turanian	VNP	SPN	*	
Onthophagus fracticornis (Preyss.)	South-centro-Euro-Anatolico-Caucasian	VNP	SPN	* *	* * * *
Onthophagus lemur (Fab.)	South-centro-Euro-Turanian	VNP	GR	* *	* * *
Onthophagus vacca (L.)	South-centro-Euro-Turanian and Maghreb	VNP	GR	*	
Onthophagus nuchicornis (L.)	South-centro-Eurasian		SPN	* *	
Onthophagus gibbulus Pall.	East-Eurasian		SPN	* *	
GEOTRUPIDAE					
Geotrupes stercorarius (L.)	Euro-Turanian	VNP	SPN	* *	* * *
Anoplotrupes stercorosus (Scriba)	European	VNP	SPN	* *	* * *
Trypocopris vernalis (L.)	Mid-Euro-Anatolico-Caucasian		SPN	* *	* * * *
Trypocopris alpinus (Hag.)	West-Alpine	VNP	SPN	* *	* * * *
Trypocopris pyrenaeus (Charp.)	West-South-centro-European		SPN	* *	

Eight main sites ranging in altitude from 1750 to 2960 m were sampled (Lumaret & Stiernet, 1991).

At each site, ten dung-baited pitfall traps were set up, each consisting of a collecting pot covered with a screen supporting the bait (200-250 g fresh weight). The dung used as a bait was from the dominant livestock occurring at each site, namely sheep droppings in subnival and nival levels and cattle pats at lower altitude. Beetles falling into the pot were killed in a water and formalin (0.5%) mixture.

The richness of the dung beetle fauna is supported by the range of climatic conditions and abundance as well as diversity of the large mammal fauna living there throughout the year. In summer, the specific richness varied according to the sites, but remained high along the whole altitudinal cline, except in the highest sites (exceeding 2700 m) where it was very low (six species at 2760 m and only three when reaching 2960 m). However, abundance remained important whatever the altitude.

Specific diversity, expressed by the Shannon-Weaver index H', and chiefly equitability E (E = H'/H'max), give a good idea of the structure and organization of the dung beetle communities and allow site classification. According to Daget (1976), the number of species in a community depends on the stability of the environmental conditions. Stable environments may induce more ecological niches than variable situations and might contain more numerous species arranged in more complex communities.

In Vanoise, the diversity index H' is high in middle altitudes during the whole of the beetle activity period. The diversity index rapidly decreases as

Table IV - Comparison of 7 sites in the Vanoise NP.
N = number of species; H' = Shannon-Weaver index; E = equitability.

Sites	Altitude (m)	Individuals	N	H'	E
Bessans	1750	4702	20	3.10	0.72
Bonneval	1960	5733	17	1.79	0.44
La Ramasse	2000	2342	11	2.05	0.59
Grand Plan	2230	5398	11	2.01	0.58
Pont du Montet	2410	3980	11	1.72	0.50
Les Roches	2440	15737	16	0.93	0.23
Balcon du Montet	2760	5252	6	0.56	0.22

the altitude increases, and the equitability index (E) varies in the same way (Tab IV and Fig. 1). The high estival values of E in the lowest sites (from 0.77 to 0.72) correspond to a model of species assemblage where equilibrium between species is well balanced. These species constitute subalpine communities whose altitudinal range corresponds to the subalpine zone defined by Gams (1935) for vegetation.

In higher sites, the abrupt decrease in the equitability index values expresses the significant dominance of a few species among the insect community. These species take advantage of most of the available dung whereas the other species are represented by only few individuals. These low values characterize young communities (pioneers), in which the species show a high power of multiplication. The lowest values (E ranging from 0.22 to 0.23, in August) correspond to subnival and nival sites.

All the species assemblages in the Vanoise are log-linear types and may be fitted to Motomura's model (Motomura, 1932), with a coefficient of linear correlation r ranging from $r = -0.96$ to $r = -0.99$ for the estival arrangements. The slopes of the graphs vary according to the sites, the highest values being those corresponding to the highest sites. When drawing all these curves on the same graph, the species assemblages which have been identified previously from the values of the equitability index can easily be recognized, with three main curve families (Fig. 2):

1) the subalpine dung beetle communities (e.g. Traribon and Bessans

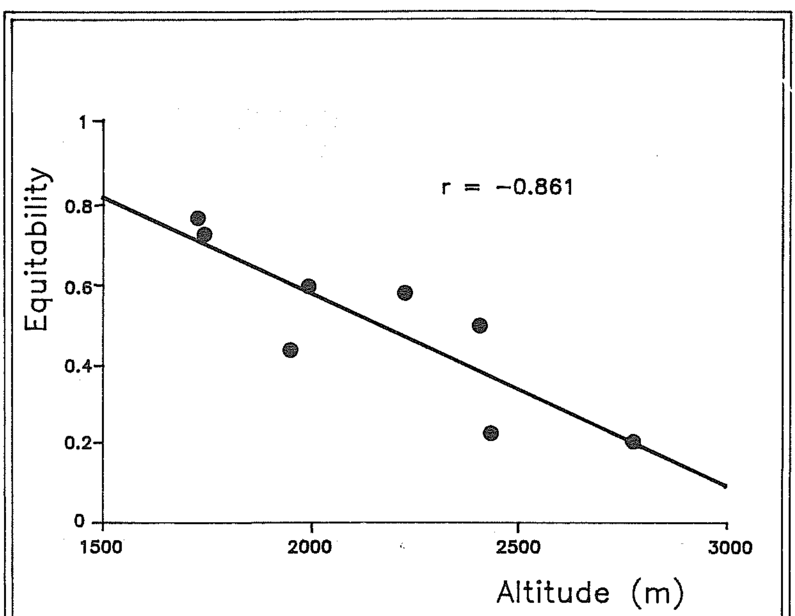

Figure 1 - Variations of equitability (E) according to altitude (m).

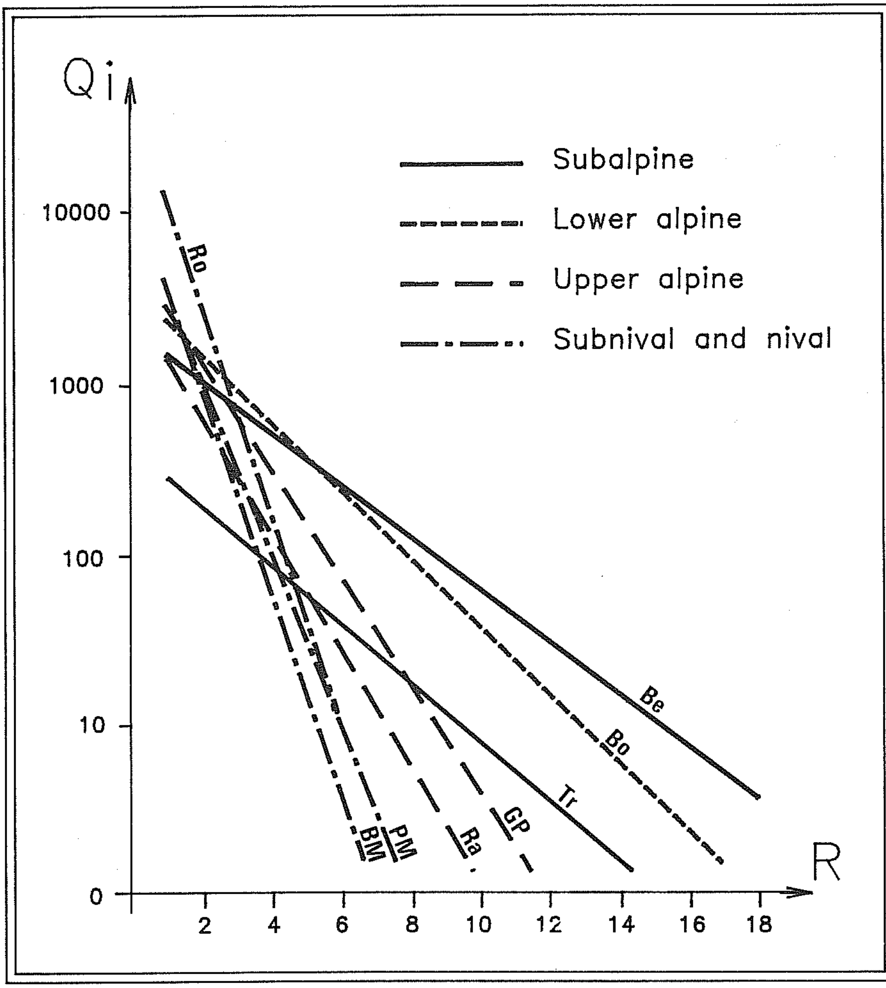

Figure 2 - Adjustments of species assemblages to Motomura's model (summer communities). Bessans (Be), Traribon (Tr), Bonneval (Bo), La Ramasse (Ra), Grand Plan (GP), Pont du Montet (PM), Les Roches (Ro), Balcon du Montet (BM).
R = rank order of species
Q_i = abundance of species

sites), with a high specific richness and a well balanced assessment of the insect numbers

2) the upper alpine communities (e.g. Grand Plan and La Ramasse sites), with less species than in the previous samples

3) the subnival and nival communities (e.g. Les Roches, Pont du Montet, Balcon du Montet, Col de Gontière), where a single species predominates.

The lower alpine communities (e.g. Bonneval site), with a high specific richness but a low equitability index due to a relative unbalance between the species frequencies, look like transitional assemblage between subalpine and upper alpine communities.

The Aphodiidae family represents the dominant group whatever the season and the community. The Scarabaeidae species, which are not very abundant, often constitute a minor group, except in the lower alpine sites where their biomass may reach up to 58% in autumn. Geotrupidae, whose total number is always very low, however may constitute a very important group when considering their biomass, except in the subnival and nival zones.

The dynamics of dung beetle communities can easily be explained both by the successive seasonal emergence of species and by their ability to compete for dung resources. Climatic constraints, mainly low temperatures and snow cover, restrict the favourable period for insects to a few months.

As a response, high montane dung beetles have adopted several tactics to ensure success in their biological cycle and to limit interspecific competition. One of these tactics consists of being ready to very rapidly exploit the dung resource when this becomes available (i.e. as soon as the snow has thawed). Consequently many dung beetles hibernate in the adult stage, as do those of the first wave of emergence. In that case snow cover acts as an effective blanket which prevents ground freezing during winter. Other tactics are to shorten the breeding time and to have an exploding demography which restricts the relative number of the other species during that period.

These tactics allow successive core species to develop during the favourable period. The percentage similarities of the successive monthly species assemblages are only about 30%, indicating extensive seasonal turnover in species (Tab. V). For a subalpine community (Bessans), table VI clearly shows the four successive waves of species replacing each other from spring to autumn, where eleven common species out of the twenty-two local species form the core of the assemblage. In lower alpine communities, only three seasonal waves of species were recorded. At mid- and high altitudes, two types of community organization can be distinguished: (1) species emerge in a rapid succession, but with little overlap between the peaks of emergence (upper alpine communities); (2) species emerge synchronously in summer, with prolonged activity in autumn (subnival and nival communities). The species composition of the upper alpine communities does not change much from spring to early autumn, although the species composition may vary from one site to another. In the highest sites (nival level), a community of six or seven species is dominated by one species (*A. obscurus*), representing from 92% to 96% of individuals at any time (Tab. VII).

4. CONCLUSION

At high altitudes, climatic constraints, in particular low temperatures and long-lasting snow cover, restrict the favorable season for dung beetles to a few months. High-montane dung beetles exhibit several adaptations to enable them to complete their life cycle in the short period of time available.

Table V - Percentage similarities of the successive monthly species assemblages at the seven study sites in Vanoise. The three columns compare the species composition in June vs. July, July vs. August and August vs. September.

Site	Altitude	Level	Percentage similarities Jun-Jul	Jul-Aug	Aug-Sept
1	1750 m	subalpine	32.3	31.7	22.2
2	1960 m	lower alpine	70.2	32.4	23.7
3	2000 m	upper alpine	26.7	56.3	17.6
4	2230 m	upper alpine	33.6	72.7	22.9
5	2410 m	subnival	47.8	75.6	58.7
6	2440 m	subnival	0.0	86.8	90.1
7	2760 m	nival	0.0	86.8	88.6

One such adaptation is to be ready to rapidly exploit the resources when they become available in early summer. Species have very short breeding seasons which allow successive core species to develop during the favourable period. In spite of unceasing adjustments, the montane dung beetle communities appear strongly structured and this contributes to maintaining a high specific diversity, even at the highest sites. Such successive waves facilitate a rapid use of almost all faeces, chiefly in the subalpine and alpine zones where cattle are numerous in summer.

Table VI - Seasonal changes in the relative abundances of the core species in a subalpine community of dung beetles (Vanoise NP, Bessans site, 1750 m).

Species	June	July	August	September
A. depressus	60.7	2.8	2.7	2.2
A. erraticus	10.8	25.8	5.1	4.2
A. pusillus	8.1	30.3	1.3	0.3
A. haemorrhoidalis	3.0	16.8	10.6	2.4
A. obscurus	9.3	6.0	12.8	1.8
A. rufipes	0.1	3.6	24.0	2.8
E. carinatus	--	0.5	22.9	--
O. fracticornis	2.4	0.3	1.2	37.7
A. corvinus	0.8	0.8	2.0	21.7
A. fimetarius	0.8	0.3	4.5	20.1
Others	3.9	12.8	12.9	6.8
Total species	16	17	20	17
Total individuals	2584	1615	4702	722

Table VII - Seasonal changes in the relative abundances of the core species in a nival community of dung beetles (Vanoise NP, Balcon du Montet, 2760 m).

Species	June	July	August	September
A. obscurus	--	91.9	90.9	96.1
Others	--	8.1	9.1	3.9
Total species	0	7	6	6
Total individuals	0	3605	5251	773

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