# THE RELATIONSHIP BETWEEN BODY SIZE AND POPULATION ABUNDANCE IN SUMMER DUNG BEETLE COMMUNITIES OF SOUTH-EUROPEAN MOUNTAINS (COLEOPTERA: SCARABAEOIDEA)

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## RÉSUMÉ

La relation entre la taille corporelle et la densité de population au sein des communautés de bousiers a été étudiée dans trois massifs montagneux sud-européens: les Alpes méridionales (France), les Pyrénées orientales (France) et la Sierra de Gredos (Espagne). Les espèces de taille moyenne dominent dans les Alpes et la Sierra de Gredos, tandis que dans les Pyrénées ce sont les espèces de grande taille (Geotrupinae) qui présentent les plus fortes densités de population. Parallèlement à la domination des espèces de grande taille les communautés des Pyrénées sont caractérisées par une très faible diversité (sous-représentation des Aphodiinae et des Coprinae). Nos résultats montrent que la relation entre la taille corporelle et la densité de population ne présente pas un patron homogène dans les communautés de bousiers du sud de l'Europe. L'étude des peuplements locaux ne peut donc permettre de déduire d'éventuelles tendances évolutives. En outre, dans les Pyrénées, la compétition interspécifique semble avoir joué un rôle important dans la mise en place de la faune. Trois hypothèses sont proposées pour expliquer la spécificité des communautés pyrénéennes.

## SUMMARY

The relationship between body size and population abundance was studied in summer dung beetle communities of three South-European mountains: southern Alps (France), eastern Pyrenees (France), Sierra de Gredos (Spain). Middle-sized species dominated in southern Alps and in the Sierra de Gredos, but the large-bodied species (Geotrupinae) presented the highest population densities in the Pyrenean communities. The domination of large-bodied species in the Pyrenees was linked with a noteworthy low diversity (under-representation of Aphodiinae and Coprinae). Our results showed (i) that the relationship between body size and population density does not present a homogeneous pattern in South-European dung beetle communities. So, the study of local assemblages does not allow to infer underlying evolutionary trends. (ii) Conversely this analysis allows to assume that interspecific competition played a main role in the formation of the Pyrenean fauna. Three hypotheses are proposed to explain the specificity of Pyrenean communities.

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# INTRODUCTION

The relationship between population abundance and body size in animals has been intensely studied since it was proposed (Damuth, 1981) that, as the large-bodied terrestrial herbivorous mammal species have lower population densities than smaller species, the amount of energy consumed by a species is independent of its body size ("Energetic Equivalence Rule"; see Cotgreave, 1993, and Blackburn & Gaston, 1999, for synthesis). This seductive theory has been largely questioned both for the form and for the heart. If in high taxonomical levels (e.g. across families) of British birds, abundance and body size are negatively correlated, they are positively correlated when closely related taxa are studied (Nee *et al.*, 1991). In terrestrial herbivorous mammals, intertidal invertebrates (Marquet *et al.*, 1995), or grassland arthropods (Sieman *et al.*, 1999), the species with intermediate body size have the highest population densities. In fact, the disparity of results is largely due to the heterogeneity of data, some studies being based on bibliographical syntheses, whereas others analyse true ecological communities (Blackburn & Gaston, 1997).

The interest of a study of the abundance-body size relationship across species within communities is twofold. First, it could help us to understand the mode of resource partitioning across interactive species. As large-bodied species have higher per capita energetic requirements than small species, they must optimize their energy supply to have population density similar to the one of small species (Blackburn & Gaston, 1999). The study of the relationship between body size and abundance may also allow us to estimate the intensity and the possible evolutionary consequences of the interspecific competition (Blackburn & Gaston, 1999).

Dung beetles (Geotrupinae, Aphodiinae, Scarabaeinae and Coprinae) constitute ecological communities since all species use similar food resource (Hanski, 1991). The abundance–body size relationship within dung beetle communities have been studied both in South Africa (Blackburn *et al.*, 1993; Chown & Steenkamp, 1996) and in Ivory Coast (Cambefort, 1994). In all cases the body size of beetles and their abundance were negatively correlated, but with a weak slope (approximately - 0.2 / - 0.6), and the large-bodied species appropriated a higher proportion of the overall amount of resource available. The occurrence of large-bodied dung beetles was conditioned by the presence of large mammals which offer big dung storages (Cambefort, 1994). Localized in warm and dry areas, the dung beetle communities in savannas are very different from temperate communities, particularly from European communities (Hanski & Cambefort, 1991). The diversity of tropical communities is higher, with many Scarabaeinae and Coprinae species.

The relationship between body size and population abundance in dung beetles has never been studied specifically in Southern Europe in spite of its original faunistical characteristics which make the analysis potentially interesting. The contact between a sub-tropical fauna, with Scarabaeinae and Coprinae, and a temperate fauna, with Geotrupinae and Aphodiinae, keeps the diversity relatively high (Cambefort, 1991). Consequently both large (Scarabaeinae, Geotrupinae) and small-bodied species (Coprinae, Aphodiinae) are present together within the communities (Lumaret & Kirk, 1987; Lumaret, 1990; Lumaret & Kirk, 1991).

In the present work, we examine the relationship between body size and population abundance in the summer dung beetle communities of three mountain ranges of Southern Europe. The comparative study permits:

— to identify the modes of the abundance-body size relationship;

    — to show whether these modes are the same in all the communities or whether each massif or community presents its own characteristics;

    — to understand the relationship between the resource partitioning and the species body size in dung beetles.

<center>MATERIAL AND METHODS</center>

SAMPLING DATA

The studied massifs were the southern Alps, the eastern Pyrenees (France), and the Sierra de Gredos (Spain). These massifs stand on a straight NE/SW 1 000 km line between 44°N and 40°N in latitude (Fig. 1). Four elevation levels were sampled in the Alps (upper montane, subalpine, lower alpine and upper alpine), three in the Pyrenees (subalpine, lower alpine and upper alpine), and three in the Sierra de Gredos (upper montane, subalpine and lower alpine). One community was sampled per elevation level.

In the Alps, the upper montane level (1 450 m a.s.l.) and the subalpine level (1 710 m) were sampled in June 1994, whereas the lower alpine level (2 030 m) and the upper alpine level (2 330 m) were sampled in July 1994. In the Pyrenees, the
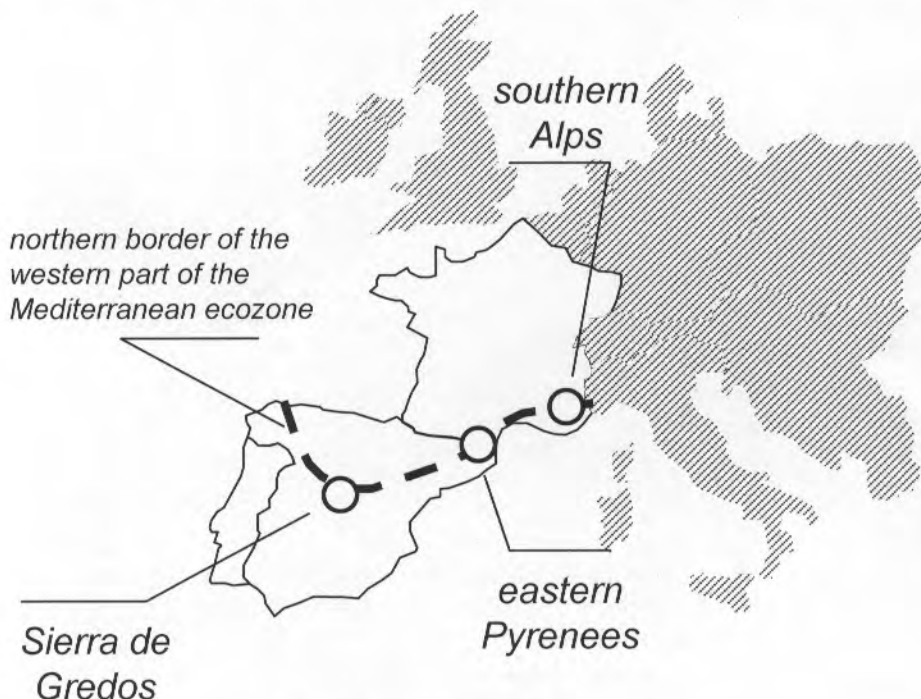


Figure 1.– Location of the studied massifs.

lower alpine level (2 060 m) and the upper alpine level (2 310 m) were sampled in
June 1998, whereas the subalpine level (1 670 m) was sampled in August 1998. In
the Sierra de Gredos, the upper montane level (1 500 m), the subalpine level
(1 720 m) and the lower alpine level (2 000 m) were sampled in June 1985.

In the Alps and the Pyrenees dung beetles were trapped using cattle dung bai-
ted traps set up in open pastures for 72 hours, each elevation level being sampled
with four traps. The pitfall design corresponded to the CSR model described in
Lobo *et al.* (1988) and Veiga *et al.* (1989): each trap consisted of a plastic basin
210 mm in diameter buried to its rim in the soil, containing a water-formalin-liquid
soap mixture. Fresh dung (1 kg) was supported on a wire grid at the top of a bucket.

In the Sierra de Gredos, three standardized dung pads (1.5 kg) set up in open
pastures were used to sample each altitudinal level. Pads and the underlying soil to
a depth of ca 10 cm (more, if galleries of paracoprids were observed) were collected
after 48 hours of exposure. Beetles were extracted from dung and soil in the labo-
ratory. Finn & Giller (2000) showed i) that dung beetle biomass sampled was at a
maximum on the second day after the deposition of baits; ii) that the relationship
between different dung sizes and dung beetle biomass was similar for pitfall trap
and dung pad samples, indicating that the colonization of dung by beetles is largely
related to immigration processes and that the proportion of species in both samples
(pads vs traps) are comparable.

In all sites, trapping, which was made when most dung beetle montane species
were active, gives a good estimate of the population densities and consequently of
the composition and structure of communities (Cambefort, 1994; Lobo *et al.*, 1998).


DATA ANALYSIS


The body size of species was expressed in dry weight (d.w.). The dry weight
of 53 out of 59 sampled species was already known (Lumaret & Kirk, 1987; Lobo,
1992; Lumaret unpublished). For the 6 other species, the dry weight ($M$) was esti-
mated by the length ($L$): *Aphodius*: $M = 0.3238$ e $^{0.4302\,L}$ ($r^2 = 0.86$); *Onthophagus*:
$M = 1.0377$ e $^{0.3568\,L}$ ($r^2 = 0.81$).

Frequency distributions of body size were determined for each massif using a
geometric progression of ratio 2.

The relative energy consumption of each species was estimated by its total bio-
mass (individual d.w. of the species * number of specimens), and by the estimation
of its metabolic rate. To assess the individual daily energy requirements ($E$) of dung
beetle species, we used the formula proposed by Brown & Maurer (1989); as did
Cambefort (1994) in tropical savannas: $E = k * M^{0.67}$ where $M$ is the body mass of
species.

As dung beetles constitute a taxonomic homogeneous group, $k$ may be assu-
med to be the same for all the species. Consequently multiplying $E$ by the number
of individuals gives a good estimate of energy used by species (Cambefort, 1994).

All the linear regressions (abundance-body size, total biomass-body size,
energy use-body size) have been computed using the ordinary least squares method
after $\log_{10}$ data transformation.

# RESULTS

17,552 specimens and 59 species have been collected in the three massifs (Table I). The highest diversity was observed in the Sierra de Gredos (34 species in 3 elevation levels); conversely the lowest biomass was collected in this massif (4 742.6 mg d.w. per trap). The diversity in the Alps was slightly lower (32 species in 4 elevation levels) but biomass per trap was twice as much (9 540.4 d.w. mg). The Pyrenees showed both the lowest diversity (14 species in 3 elevation levels) and the highest biomass (14 885.5 d.w. mg per trap).

## TABLE I

*Numbers and body sizes of dung beetles trapped (length in mm, dry weight in mg). (1) Lumaret & Kirk (1987); (2) Lobo (1992); (3) Lumaret unpublished; * length from Lumaret & Kirk (1987) or Lumaret (1990) and estimated dry weight; ** same values than* E. fulvus

| | southern Alps | | | | eastern Pyrenees | | | Sierra de Gredos | | | body size | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | u. mon. | sub. | l. alp. | u. alp. | sub. | l. alp. | u. alp. | u. mon. | sub. | l. alp. | length | dry weight | |
| **GEOTRUPINAE** | | | | | | | | | | | | | |
| Anoplotrupes stercorosus Scriba | | 1 | | | 51 | 77 | 45 | | | | 18.54 | 174.21 | (2) |
| Geotrupes ibericus Baraud | | | | | | | | | 5 | 2 | 21.84 | 264.81 | (2) |
| Geotrupes spiniger Marsham | | | | | 1 | | | | | | 22 | 386.9 | (1) |
| Geotrupes stercorarius (Linné) | 26 | 44 | | 3 | 51 | 50 | 34 | | | 1 | 23.24 | 316.34 | (2) |
| Sericotrupes niger (Marsham) | | | | | | | | 2 | 1 | | 20.6 | 228.14 | (2) |
| Trypocopris pyrenaeus Charpentier | | | | | 98 | 417 | 75 | | | | 17.89 | 174.34 | (2) |
| Trypocopris vernalis (Linné) | 95 | 199 | 7 | | | | | | | | 15.9 | 119.5 | (1) |
| **APHODIINAE** | | | | | | | | | | | | | |
| Aphodius depressus (Kugelann) | | 106 | | 5 | | | | | | | 7.5 | 6.5 | (3) |
| A. luridus (Fabricius) | 2 | 1 | | | | | | | | | 8.2 | 12.1 | (1) |
| A. rufipes (Linné) | | | | 1 | 7 | 23 | 7 | | | | 12 | 19.8 | (3) |
| A. satyrus Reitter | | 8 | 3 | 141 | | | | | | | 6.25 | 4.5 | (3) |
| A. abdominalis Bonelli | | | | 48 | | 2 | 7 | | | | 5 | 3.74 | (3) |
| A. bonvouloiri Harold | | | | | | | | 24 | 64 | 800 | 7.89 | 7.21 | (2) |
| A. scybalarius (Fabricius) | | | | 3 | 25 | 1 | | | | | 6 | 4.5 | (3) |
| A. immaturus Mulsant | | 3 | | 563 | | | | | | | 7.5 | 6 | (3) |
| A. obscurus (Fabricius) | 4 | 209 | 105 | 4624 | | 21 | 202 | | | | 7.25 | 5.9 | (3) |
| A. aestivalis Stephens | | | | | 10 | | | | | | 7.5 | 11.67 | (3) |
| A. fimetarius (Linné) | 182 | 142 | 18 | 101 | | 1 | | 9 | 9 | 19 | 6.5 | 9.9 | (1) |
| A. foetidus (Herbst) | | | | | | | | 94 | 64 | 2 | 6.4 | 6.8 | (1) |
| A. granarius Erichson | | 5 | | 2 | | | | 1 | 4 | | 4 | 3.4 | (1) |
| A. lineolatus Illiger | | | | | | | | 1 | 1 | | 4.59 | 2.33 | * |
| A. erraticus (Linné) | 61 | 31 | 17 | 112 | | | | 2 | | | 7.5 | 8 | (1) |
| A. scrutator (Herbst) | | | | | | | | 90 | 36 | 3 | 11.1 | 40.8 | (1) |
| A. pusillus (Herbst) | 425 | 325 | 4 | 5 | | | 1 | | | | 3 | 1.3 | (1) |
| A. merdarius (Fabricius) | | | | | | | | 3 | | | 4.5 | 0.9 | (1) |

TABLE I (continued)

| | southern Alps | | | | eastern Pyrenees | | | Sierra de Gredos | | | body size | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | u. mon. | sub. | l. alp. | u. alp. | sub. | l. alp. | u. alp. | u. mon. | sub. | l. alp. | length | dry weight | |
| A. coenosus (Panzer) | | | | | | | | | 1 | | 4.71 | 2.46 | * |
| A. paracoenosus Balthasar & Hrubant | 6 | | | | | | | | | | 3.6 | 2.3 | (1) |
| A. striatulus Waltl | | | | | | | | 1 | | | 3.47 | 1.44 | * |
| A. consputus Creutzer | | | | | | | | | 24 | | 3.9 | 1.8 | (1) |
| A. prodromus (Brahm) | 1 | | | | | | | | | | 6.1 | 4.9 | (1) |
| A. alpinus (Scopoli) | | | | 54 | 6 | 2 | | | | | 6 | 3.4 | (3) |
| A. haemorrhoidalis (Linné) | 16 | 11 | 2 | 106 | 7 | 3 | | | 2 | | 4.6 | 4 | (1) |
| A. corvinus Erichson | 1 | | | 9 | | | | | | | 3.5 | 1.3 | (3) |
| A. biguttatus Germar | 5 | | | | | | | | | | 2.8 | 0.6 | (1) |
| A. quadrimaculatus (Linné) | 1 | | | | | | | | | | 3.2 | 0.8 | (1) |
| A. borealis Gyllenhal | 2 | | | | | | | | | | 3.7 | 1.59 | * |
| A. uliginosus (Hardy) | 2 | 2 | 2 | | | | | | | | 4 | 1.7 | (3) |
| A. fossor (Linné) | 7 | | 1 | 2 | | | | | | | 11.5 | 41 | (3) |
| A. scrofa (Fabricius) | | | | | | | | | | 2 | 3.2 | 1.4 | (1) |
| SCARABAEINAE | | | | | | | | | | | | | |
| Gymnopleurus flagellatus (Fabricius) | | | | | | | | | 1 | | 9.7 | 102 | (1) |
| Scarabaeus laticollis (Linné) | | | | | | | | | 1 | | 20 | 172.9 | (1) |
| COPRINAE | | | | | | | | | | | | | |
| Caccobius schreberi (Linné) | | | | | | | | 6 | 4 | | 5.5 | 7.1 | (1) |
| Copris lunaris (Linné) | | | | | | | | 9 | 9 | | 18 | 228 | (1) |
| Euoniticellus fulvus (Goeze) | 1 | | | | | | | 10 | 3 | 29 | 9 | 25.1 | (1) |
| Euoniticellus pallipes (Fabricius) | | | | | | | | 1 | | | 9 | 25.1 | ** |
| Euonthophagus amyntas (Olivier) | | | | | | | | | 1 | 1 | 7.5 | 27 | (1) |
| Euonthophagus gibbosus (Scriba) | 1 | | | | | | | | | | 10.5 | 22.5 | (1) |
| Onthophagus furcatus (Fabricius) | | | | | | | | 4 | 8 | | 3.7 | 3.7 | (1) |
| O. taurus (Schreber) | | | | | | | | 20 | 8 | | 8.5 | 32.4 | (1) |
| O. baraudi Nicolas | 5 | 372 | 738 | 1 | | | | | | | 6 | 7.5 | (3) |
| O. fracticornis (Preyssler) | 781 | 1211 | 1884 | 52 | 11 | 2 | 1 | 7 | 1 | | 8.5 | 10 | (3) |
| O. grossepunctatus Reitter | | | | | | | | 2 | | 1 | 4.5 | 5 | (1) |
| O. joannae Goljan | 133 | 70 | 1 | | | | | 4 | 115 | 1 | 4.7 | 6.2 | (1) |
| O. lemur (Fabricius) | 22 | | 16 | | | | | 155 | 127 | 171 | 6.5 | 13.4 | (1) |
| O. similis (Scriba) | | | | | | | | 298 | 452 | 48 | 5.5 | 5 | (3) |
| O. stylocerus (Graëlls) | | | | | | | | 5 | 72 | 82 | 10.5 | 43.97 | * |
| O. vacca (Linné) | | | | | | | | 5 | | 5 | 10 | 41.2 | (1) |
| O. verticicornis (Laicharting) | 61 | 2 | 11 | | | | | 10 | 4 | | 7.6 | 18.7 | (1) |
| O. maki (Illiger) | | | | | | | | 109 | 35 | | 5.5 | 10.5 | (1) |
| no individuals | 1840 | 2742 | 2809 | 5832 | 254 | 607 | 377 | 872 | 1052 | 1167 | | | |
| no species | 23 | 18 | 14 | 18 | 8 | 11 | 10 | 25 | 26 | 15 | | | |
| dry weight (mg) | 33004 | 57374 | 26643 | 35626 | 42968 | 102601 | 33057 | 13518 | 15116 | 14050 | | | |

The faunas in eastern Pyrenees and in southern Alps were very similar, with only 3 Pyrenean species which have not been trapped in the Alps (*Geotrupes spiniger*, *Trypocopris pyrenaeus* and *Aphodius aestivalis*)(Table I). When species were arranged in decreasing order of abundance, the rankings obtained in the Alps and in the Pyrenees were correlated (Spearman rank correlation $r_s = 0.303$; $P = 0.021$). The faunistical composition in the Sierra de Gredos was markedly different: only 10 Iberian species out of 34 were present in the Alps and 2 in the Pyrenees (Table I). Morevover the abundance of species in the Sierra de Gredos was inversely proportional to their abundance in the Alps and in the Pyrenees (respectively: $r_s = -0.392$; $P = 0.003$; and $r_s = -0.339$; $P = 0.010$). These differences in faunistical composition had low consequences for the diversity of each sub-family among the massifs (Table II), but high differences were always observed when the numerical abundances of sub-families (number of specimens) were considered (Table III). The eastern Pyrenees appeared very particular. Geotrupinae were very abundant in the Pyrenees whereas they were restricted to the lowest elevation level in the Alps and they were nearly missing in the Sierra de Gredos. Aphodiinae, which were always abundant in the Alps and in the Sierra de Gredos, were numerous only in the upper alpine pyrenean level. Coprinae, which were dominant up to the subalpine level in the Sierra de Gredos and up to the lower alpine level in the Alps, were nearly missing in the Pyrenees.

TABLE II

*Species diversity of dung beetle sub-families in elevation levels*

| Level | Massif | Geotrupinae | Aphodiinae | Scarabaeinae | Coprinae | $\chi^2$ | P |
|---|---|---|---|---|---|---|---|
| Upper montane | Alps | 2 | 14 | 0 | 7 | 4.25 | 0.119 |
| | Gredos | 1 | 9 | 0 | 15 | | |
| Subalpine | Alps | 3 | 11 | 0 | 4 | 13.83 | 0.032 |
| | Pyrenees | 4 | 3 | 0 | 1 | | |
| | Gredos | 2 | 9 | 2 | 13 | | |
| Lower alpine | Alps | 1 | 8 | 0 | 5 | 6.65 | 0.15 |
| | Pyrenees | 3 | 7 | 0 | 1 | | |
| | Gredos | 2 | 5 | 0 | 8 | | |
| Upper alpine | Alps | 1 | 15 | 0 | 2 | 3.16 | 0.206 |
| | Pyrenees | 3 | 6 | 0 | 1 | | |

The distribution of species according to their dry weight was not significantly different among the three massifs ($\chi^2 = 12.98$; $P = 0.674$) (Fig. 2), and the body size of species across massifs showed no significant difference (Kruskal-Wallis test: $H = 2.860$; $P = 0.239$). Most species body sizes ranged from 3.13 mg to 12.5 mg (dry weight) in the Alps and in the Pyrenees (respectively 16 species out of 32, and 8 species out of 14), and from 3.13 mg to 50 mg in the Sierra de Gredos (22 species out of 34).
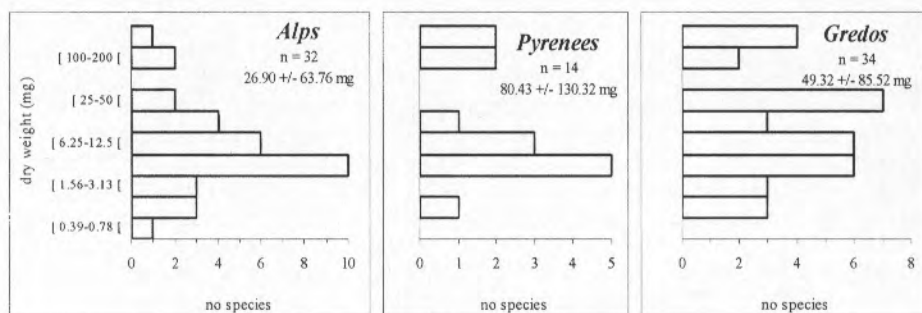
Figure 2.– Distribution of species according to their dry weight.

## TABLE III

*Numerical abundance of dung beetle sub-families in elevation levels*

| Level | Massif | Geotrupinae | Aphodiinae | Scarabaeinae | Coprinae | $\chi^2$ | P |
|---|---|---|---|---|---|---|---|
| Upper montane | Alps | 121 | 715 | 0 | 1004 | 118.27 | < 0.0001 |
| | Gredos | 2 | 225 | 0 | 645 | | |
| Subalpine | Alps | 244 | 843 | 0 | 1655 | 1415.46 | < 0.0001 |
| | Pyrenees | 201 | 42 | 0 | 11 | | |
| | Gredos | 6 | 205 | 2 | 839 | | |
| Lower alpine | Alps | 7 | 152 | 0 | 2650 | 6074.56 | < 0.0001 |
| | Pyrenees | 544 | 61 | 0 | 2 | | |
| | Gredos | 3 | 826 | 0 | 338 | | |
| Upper alpine | Alps | 3 | 5776 | 0 | 53 | 1267.93 | < 0.0001 |
| | Pyrenees | 154 | 222 | 0 | 1 | | |

In the communities of the Alps and of the Sierra de Gredos, there was no correlation between body size and the number of specimens (log values; $P > 0.25$; Table IV). In these massifs, middle-sized species showed the highest population densities (Fig. 3). Conversely abundance and body size were positively correlated in the lower alpine and upper alpine Pyrenean levels. A positive correlation was also observed in the subalpine level of the Pyrenees when the single trapped specimen of *Geotrupes spiniger* was excluded from the calculation ($r^2 = 0.568$; $P = 0.050$; slope = 1.278).

TABLE IV

*Regression of species numerical abundance on body weight (mg dry weight) (log values), and slope of regression lines (ordinary least squares) (NS: not significantly different from 0)*

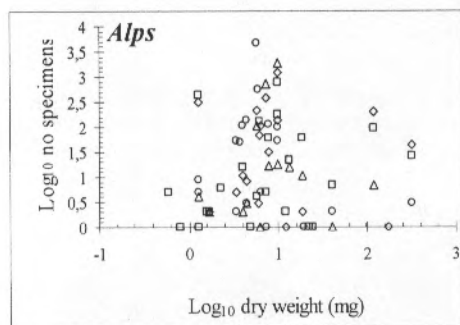| Massif | Level | n° species | $r^2$ | P | Slope |
|--------|-------|-----------|-------|---|-------|
| Alps | upper montane | 23 | 0.061 | 0.256 | NS |
| | subalpine | 18 | 0.004 | 0.800 | NS |
| | lower alpine | 14 | 0.004 | 0.828 | NS |
| | upper alpine | 18 | 0.053 | 0.356 | NS |
| Pyrenees | subalpine | 8 | 0.004 | 0.881 | NS |
| | lower alpine | 11 | 0.615 | 0.004 | 0.886 |
| | upper alpine | 10 | 0.387 | 0.055 | 0.598 |
| Gredos | upper montane | 25 | 0.025 | 0.448 | NS |
| | subalpine | 26 | 0.047 | 0.288 | NS |
| | lower alpine | 15 | 0.027 | 0.561 | NS |
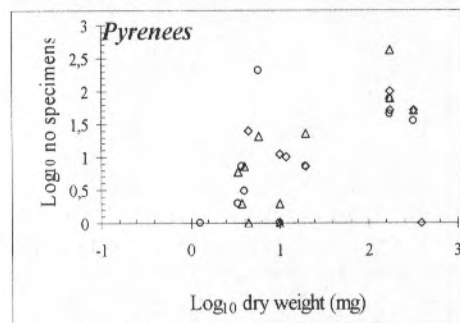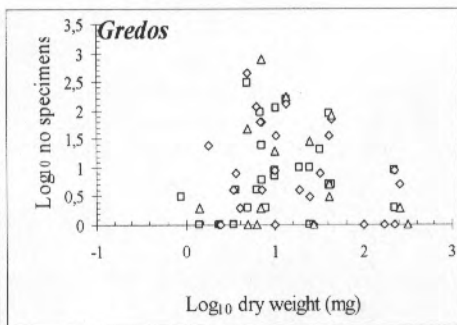


Figure 3.– Relationship between species numerical abundance and species dry weight (mg) (log values) (square: upper montane; diamond: subalpine; triangle: lower alpine; circle: upper alpine).

Both in the Alps and in the Sierra de Gredos body size and total biomass of species were positively correlated in the upper montane and subalpine levels (Table V); the correlation was not significant in the lower alpine and upper alpine levels. In the Pyrenees the correlation was both significant and pronounced all along the elevation gradient.

TABLE V

*Regression of species biomass abundance on body weight (mg dry weight) (log values), and slope of regression lines (ordinary least squares) (NS: not significantly different from 0)*

| Massif | Level | $r^2$ | P | Slope |
|---|---|---|---|---|
| Alps | upper montane<br>subalpine<br>lower alpine<br>upper alpine | 0.507<br>0.262<br>0.244<br>0.086 | 0.0001<br>0.030<br>0.072<br>0.238 | 1.335<br>0.902<br>NS<br>NS |
| Pyrenees | subalpine<br>lower alpine<br>upper alpine | 0.622<br>0.878<br>0.818 | 0.020<br>< 0.0001<br>0.0003 | 1.052<br>1.886<br>1.598 |
| Gredos | upper montane<br>subalpine<br>lower alpine | 0.488<br>0.278<br>0.220 | 0.0001<br>0.006<br>0.078 | 1.197<br>0.736<br>NS |

Both in the Alps and the Sierra de Gredos a positive correlation between body size and energy consumption by species was only observed in the upper montane level (Table VI), whereas at higher altitudes most of trophic resources were con-

TABLE VI

*Regression of relative energy use on body weight (mg dry weight) (log values), and slope of regression lines (ordinary least squares) (NS: not significantly different from 0)*

| Massif | Level | $r^2$ | P | Slope |
|---|---|---|---|---|
| Alps | upper montane<br>subalpine<br>lower alpine<br>upper alpine | 0.368<br>0.126<br>0.139<br>0.016 | 0.002<br>0.150<br>0.189<br>0.618 | 0.366<br>NS<br>NS<br>NS |
| Pyrenees | subalpine<br>lower alpine<br>upper alpine | 0.437<br>0.831<br>0.739 | 0.074<br>0.0001<br>0.001 | NS<br>0.534<br>0.583 |
| Gredos | upper montane<br>subalpine<br>lower alpine | 0.333<br>0.105<br>0.083 | 0.003<br>0.107<br>0.298 | 0.384<br>NS<br>NS |

sumed by middle-sized species (Fig. 4). Conversely energy consumption and body size were positively correlated in the lower alpine and upper alpine Pyrenean levels, and a positive correlation could be also observed in the subalpine level when *Geotrupes spiniger* was excluded ($r^2 = 0.892$; $P = 0.001$; slope $= 0.800$).
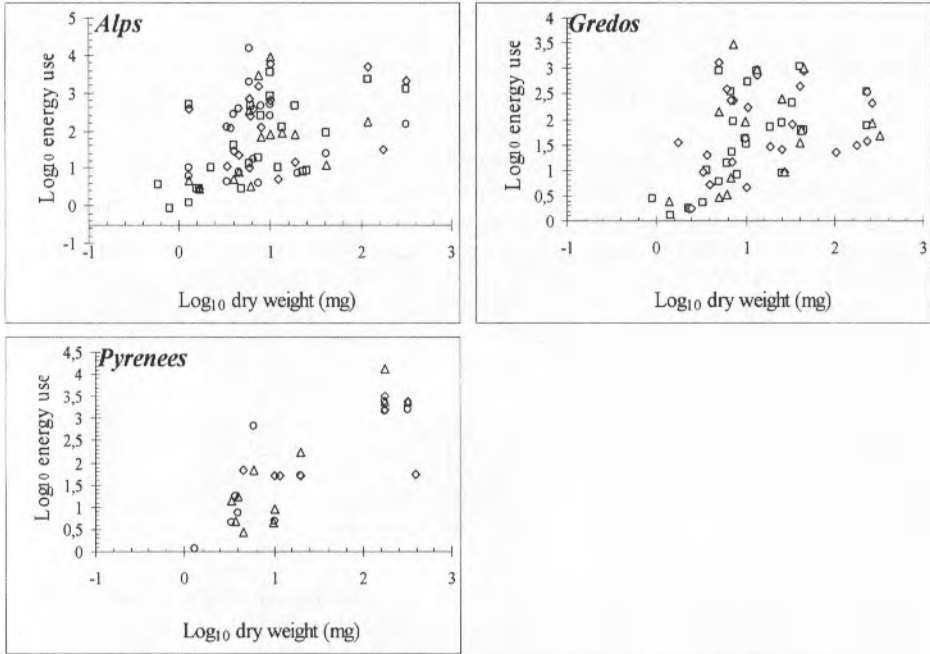


Figure 4.– Relationship between relative population energy use and species dry weight (mg) (log values) (square: upper montane; diamond: subalpine; triangle: lower alpine; circle: upper alpine).

## DISCUSSION AND CONCLUSION

The mean body size of species and their distribution into dry weight classes were similar in all the three massifs. Most species showed a medium size and the biometrical pattern was homogeneous across the massifs.

In the seven communities sampled in the southern Alps and in the Sierra de Gredos, the body size of the most abundant species was always ranged from 5 to 10 mg. Above the subalpine level in the two massifs (5 communities out of 7), most of trophic resource was consumed by middle-sized species. In the Alps and the Sierra de Gredos, where faunistical compositions were markedly different, the highest species diversity, population density and energy consumption concerned middle-sized species. These similarities could be interpreted both in a statistical and in a biological way (Blackburn & Gaston, 1999).

If there are more middle-sized species than large or small ones, as observed in the three massifs, the species of intermediate size are likely to provide the most extreme, i.e. highest, abundances (Cotgreave, 1993). But the domination of middle-sized species could also be due to ecological and evolutionary constraints which could favour an intermediate size. This hypothesis has been advanced for intertidal invertebrates, terrestrial herbivorous mammals (Marquet *et al.*, 1995) and grassland arthropods (Siemann *et al.*, 1999). If the middle-sized species appropriate a higher proportion of resource available, they can be favoured by natural selection. The highest diversity observed at a regional scale would then result from a selection still in progress in the communities.

However the analysis of the Pyrenean communities gives quite different results. In this massif, with a faunistical composition close to the Alps, the large-bodied species presented the highest population densities and consequently they appropriated a higher proportion of resource.

If the domination of middle-sized species observed in the Alps and in the Sierra de Gredos is not a general rule, one can conclude: i) that this pattern was not only due to a statistical law; ii) that the modes of the relationship between body size and population density characterize each massif: closely related faunas could show very different patterns of resource partitioning. Consequently the study of the abundance-body size relationship in the summer dung beetle communities of southern European massifs does not allow to infer underlying evolutionary trends.

The domination of large-bodied species in the Pyrenean communities was linked to a noteworthy low diversity (under-representation of Aphodiinae and Coprinae) which cannot be attributed to a sampling artefact because the mean biomass collected per trap in the Pyrenees (trapping efficiency) was 1.5 times and three times higher than in the Alps and in the Sierra de Gredos, respectively.

Either the absence of small-bodied species allowed large dung beetles to develop large populations in the Pyrenees, or the population dynamics of large-bodied species prevented small dung beetles from settling in the massif.

The first hypothesis is very unlikely because it implies the initial absence of numerous species having different ecological requirements. The second hypothesis is more probable because it is based on the presence of only three large-bodied Geotrupinae: *Anoplotrupes stercorosus*, *Geotrupes stercorarius* and *Trypocopris pyrenaeus*. Gittings & Giller (1999) showed that, in late summer in southern Ireland, the decomposition of dung pats by *Geotrupes spiniger* was too fast to allow the *Aphodius* larvae to complete their development. The study of the abundance-body size relationship allows to assume that interspecific competition played a main role in the formation of the Pyrenean fauna. The singularity of the Pyrenean pattern shows also that the intensity and the consequences of interspecific competition differed markedly across the massifs.

The challenge is now to explain the specificity of Pyrenean communities. Three hypotheses could be put forward:

(i) Trophic resources can act upon the structure of dung beetle communities. In tropical savannas the presence of large-bodied dung beetles is conditioned by the presence of large mammals which offer big dung storage (Cambefort, 1994). In the Mediterranean area the situation is more complex (Lumaret *et al.*, 1992): the communities in sheep pastureland are dominated by middle-sized tunnelers (Coprinae), whereas dwellers (Aphodiinae) dominate the communities in cattle pastureland. The change in trophic resources from sheep droppings to cattle dung pats brings about both a rise in the total biomass of large-sized tunnelers (Coprinae) and a rise

in the abundance of dwellers (Aphodiinae). The change in resources did not affect species diversity. The Eastern Pyrenees and the Sierra de Gredos are predominantly grazed by cattle, whereas sheep flocks are dominant in the Southern Alps pastures. If the abundance-body size relationship was linked to the type of livestock, the structure of dung beetle communities would be the same in the Pyrenees and in the Sierra de Gredos, with the dominance of Aphodiinae. But the patterns observed were markedly different. Consequently one can assume that the specificities of the Pyrenean communities (specially their poor diversity) were not due to the composition of livestock.

(ii) The establishment of ecological communities is both under the control of several ecological constraints and under the influence of the local history (Ricklefs & Schluter, 1993). In Europe the climatic history of Quaternary was characterized by an alternation of cooler/warmer episodes which considerably changed the distribution of species and the composition of communities (Blondel, 1995; Reille *et al.*, 1996). The populating of South-European mountains by dung beetles cannot be understood without considering this historical context (Jay-Robert *et al.*, 1997; Martín-Piera *et al.*, 1992). Unfortunately the palaeoentomological data are not sufficient to reconstruct the history of the Pyrenean massif and a fortiori to understand how the large-bodied species were favoured (Ponel *et al.*, 1999).

(iii) The ecological communities are composed of populations the dynamics of which is linked both to local and to regional factors. For example the spatial arrangement of landscape favours or penalizes species with interconnected populations (Wiens, 1997; Thomas & Kunin, 1999). The specificities of grassland Pyrenean communities should be linked with the characteristics of surrounding biotopes (scrubs, forests). This hypothesis seems to be especially relevant because the three dominant species in Pyrenean communities (*Anoplotrupes stercorosus*, *Geotrupes stercorarius* and *Trypocopris pyrenaeus*) are abundant both in scrubs and forests when trophic resource is available (Lumaret, 1990). This ability is uncommon in the European dung beetles which prefer open habitats. If the resource were more equitably distributed in the landscape in the eastern Pyrenees than in the other massifs (grazing under forests and/or many wild mammals), the Geotrupinae species may be favoured.

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