

THE DUNG BEETLES OF THE GRAN PARADISO NATIONAL PARK: A PRELIMINARY ANALYSIS (*INSECTA: COLEOPTERA: SCARABAEOIDEA*)

Borghesio L.*, Palestrini C.** & Passerin d'Entrèves P.*

* Dipartimento di Biologia Animale e dell'Uomo, Università di Torino, Via Accademia Albertina 17, 10123 - Torino

** Dipartimento di Scienze e Tecnologie Avanzate, Università del Piemonte orientale, C.so Borsalino 54, 15100 - Alessandria

Abstract - A survey of the dung beetles (Coleoptera: Scarabaeoidea) of Gran Paradiso National Park was done in 1996-97. The insects were collected directly in the dung of wild and reared mammals or by automated pitfall traps. Altogether 28 sites were sampled, at altitudes ranging from 700 to 2800 m. Thirty species of Scarabaeoidea were collected, of which 27 inside the borders of the protected area and another 3 just outside of them, at low altitude sites. The dung beetle community was dominated by Aphodiidae (20 species), while Scarabaeidae and Geotrupidae were represented by 6 and 4 species respectively. Among the species found, we remark the presence of *Aphodius pyrenaicus*, a high altitude species typical of Alpine marmot's burrows, and of *Geotrupes mutator*, whose distribution and population have strongly decreased in Europe.

Key-words: Aphodiidae, Scarabaeidae, Geotrupidae, high-altitude habitats, coprophilous fauna

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1. Introduction

The study of dung beetles communities has a remarkable interest, both from a strictly scientific point of view as from that of wildlife management, owing to the important role of these organisms as decomposers of animal wastes. Moreover, in recent times, some authors (Lumaret, 1990; Biström *et al.* 1991) suggested that the increasing abandonment of traditional stock-raising over most of the European continent could bring about deep changes in the dung insect communities, which, being deprived of the food resource which was provided by huge numbers of domestic livestock in the past, are now more and more dependent on the usually scarce wild herbivore populations.

An area like the Gran Paradiso National Park (GPNP), where significant numbers of both wild and domestic herbivores are still existent, can be an ideal subject for studying dung beetles and their links with numerous mammalian species. While in most biotopes of the European continent human activities have probably had heavy and usually negative consequences on the diversity and the ecology of the dung insect communities, we believe that within the GPNP these changes must have been slight or non-existent, and that this

area has therefore an important value for researchers.

On these grounds the GPNP has started a research program focused on the dung beetles living in its territory.

2. Study area and methods

Dung beetles were collected between March and October 1996 and 1997. Figure 1 shows the study area, which lies entirely within 1:100.000 IGM map, sheet No 41 (Gran Paradiso).

Geological substrate is mainly acidic (gneisses); basic soils, derived from calceschists, are found

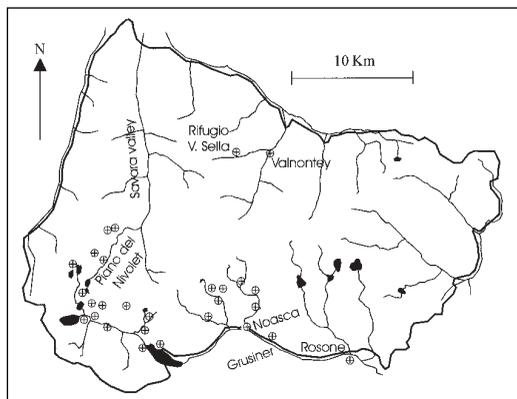


FIG. 2 - Map of the study area showing the borders of the Gran Paradiso National Park, the main stream and lakes in the area and the collection sites.

along the western slope of the Savara valley. Rainfall is quite high, being between 900 and 1500 mm/year, with mean figures for the three summer months comprised between 300 and 500 mm (De Biaggi *et al.*, 1990).

The vegetation in the study area lies within the Upper Montane, Subalpine, and Alpine levels (Pignatti, 1976). Woody vegetation comprises broad-leaved woods, dominated by chestnut (*Castanea sativa*), at lower altitudes; higher on, conifer forests with prevailing larch (*Larix decidua*) and small amounts of spruce (*Picea abies*) are found. Open areas, such as meadows and pastures are also extensive at these levels. At the highest altitudes, woody plants are replaced by herbaceous formations which are usually derived from the fitosociological class *Caricetea curvulae*.

Herbivore mammals comprise high densities of both wild and domestic species. Wild species include Alpine ibex (*Capra ibex*), chamois (*Rupicapra rupicapra*), roe deer (*Capreolus capreolus*), red deer (*Cervus claphus*), wild boar (*Sus scrofa*), and marmot (*Marmota marmota*). Domestic herbivores are mainly cattle, sheep, and a small number of goats and donkeys.

The insect collections were done in 28 places (Fig. 1), between 700 and 2800 meters. We mainly collected by direct inspection of the dung of various species of wild and domestic herbivores (Alpine Ibex, Chamois, Marmot, Wild boar, donkey, sheep, goat, cattle). Occasionally, in order to achieve a more thorough sample, we adopted pitfall traps, made of jars buried up to its upper margin in the soil, covered with a funnel which prevented insects from escaping and baited with 70 g of dung (cattle or Alpine Ibex) wrapped in a fine mesh hanging over the trap. Systematics at the species level follows Dellacasa (1983) for Aphodiidae, and Baraud (1992) for Scarabaeidae.

3. Results

Family Geotrupidae

Anoplotrupes stercorosus (Scriba 1796)

Length 12-19 mm. This species ranges over

most of Europe, and reaches the Caucasus to the East. In Italy it can be found in the whole of the Peninsula and in Sicily.

In the study area we found it up to about 1600 m, from May to October, usually in higher numbers in woody than in open habitats. We mainly found it in cattle and ibex dung (respectively 53% and 47% of specimens collected), but occasionally also in other decomposing materials, such as carrion and mushrooms. This species is not usually abundant in number, but its large size and paracoprid nesting, involving the digging of underground nests provided with dung carried from the soil surface, make it one of the species with the potentially highest ecological importance owing to its activity as a decomposer and recycler of dung-derived organic material.

Geotrupes mutator (Marshall 1802)

Length 15-24 mm. Present in most of Europe and Anatolia. In Italy it ranges over the northern and central regions, but it is seemingly absent from the lowland areas.

This species was collected in pitfall traps with bovine or ibex dung on a few occasions in the lower Orco valley (Grusiner, 980 m; Rosone, 715 m), just outside the borders of the GPNP. We believe that further research could locate it within the protected area. *Geotrupes* markedly decreased in number in Europe during the last 20 years (E. Barbero, *pers. comm.*), and its conservation certainly deserves some attention.

Geotrupes spiniger (Marshall 1802)

Length 18-26 mm. This species ranges over all Europe and Central Asia; in Italy it is found almost everywhere, but mainly in lowland areas. We found it on few occasions, in cattle dung, up to about 1700 m of altitude and from July to October.

Geotrupes stercorarius (Linnaeus 1768)

Length 16-25 mm. An European species, in Italy found up to Tuscany, in the southern part of its

range mostly in montane and alpine habitats. We found it commonly both in open and wooded habitats, mostly in cattle dung (64% of individuals collected) but also in human feces and ibex dung. It was not found in marmot and chamois dung, which are probably avoided owing to their small size compared with this species, one of the largest dung beetles in our continent. *G. stercorarius* is similar to *A. stercorosus*, in that it is a large-sized species, making up a large fraction of the biomass of the dung insect community, and probably plays an important role in the ecosystem as decomposer.

Family Aphodiidae

Aphodius (Acrossus) depressus (Kugelann 1792)
Length 6-9 mm. An Holarctic species, ranging over the whole of Italy. In the study area we found it from May to October, but mostly from May to July. It is often abundant, both in pastures and woods, between 900 and 2400 m. We collected it in various kinds of dung, including donkey, ibex, chamois and cattle.

Aphodius (Acrossus) rufipes (Linnaeus 1758)
Length 11-13 mm. This species has an Holarctic range, and it is found in the whole of the Italian peninsula, mainly in hilly and montane habitats. We collected it in fairly good numbers, from 900 up to 2200 m, between June and October. It seems to have a preference for woody habitats, especially during the hottest part of the summer. It was commonest in cattle dung (54% of individuals), but was collected in that of ibex (46%) as well.

Aphodius (Agoliinus) satyrus (Reitter 1892)
Length 5-6 mm. The range of this species lies on the Alps and the Apennines, southwards up to the Abruzzi. *A. satyrus* is usually considered a typical species of the alpine pastures above 2000 m (Dellacasa, 1983), but in the GPNP we found it from about 1400 m of altitude. However, at the lower elevations it showed a very clear preference for conifer woods. The

upper limit of its distribution is at about 2700 m, and the adults are found from June to August. *A. satyrus* was mainly found in cattle dung (65% of individuals collected) but also of ibex, chamois and sheep, and it was usually commoner in dung pats several days old than in fresh ones.

Aphodius (Agolius) abdominalis (Bonelli 1812)
Length 5-6.5 mm. A species of the high mountains of central Europe. In Italy it ranges over the entire Alpine arc, where it mainly selects high altitude pastures.

This is a fairly rare species, which we found on only few occasions in cattle, ibex and sheep dung between 2100 and 2500 m, from late May to July.

Aphodius (Agrilinus) ater (Degeer 1774)
Length 4-6 mm. This species ranges from Northern Spain to the Caucasus, Northern Europe and Siberia up to Vladivostock. It occupies all the Italian peninsula and Sicily, with a preference for sunny pasture in the plains or the hills. We mainly collected it in late spring or early summer, up to about 1000 m. It affects both open and wooded habitats, where it was found in wild boar, cattle and sheep dung. Lumaret & Stiernet (1989) state that larvae develop in underground tunnels which they dig and provide with dung brought from the soil surface.

Aphodius (Agrilinus) scybalarius (Fabricius 1792)
Length 5-7 mm. This species is found in most of the Palearctic region. In Italy it ranges over the peninsular area and Sicily. We collected this species up to 2200 m, mostly in open habitats and in cattle dung (70% of individuals), from June to October. Preliminary laboratory observations show that this species has an underground nesting behaviour similar to that of *A. obscurus* (see below).

Aphodius (Amidorus) obscurus (Fabricius 1792)
Length 6-8 mm. A mountain species ranging over central and southern Europe, from the

Pyrenees to the Carpathians, reaching the Caucasus to the east. In Italy it is distributed along the alpine arc and in some places of the Apennines, up to the Sila; it usually selects montane and sub-montane pastures.

In the GPNP it is by far the commonest species of the upper altitudes. We found it regularly from May to September, from 1500 up to 3000 m. The sometimes amazing abundance of this species is perhaps a consequence of its high ecological plasticity and of behavioural adaptations to alpine habitats. It feeds and probably breeds in all kinds of dung available (man, sheep, donkey, ibex, chamois, marmot). Adults lay eggs in underground nests dug under the dung and larval development occurs in short galleries made by the larvae, which carry small amounts of dung in these nests as a food provision (Fig. 2). The behaviour of *A. obscurus* is relatively uncommon in the genus *Aphodius*, where usually primitive non-nesting (endocoprid, *sensu* Halffter & Matthews, 1966) habits are found. In primitive situations adults lay eggs and larvae develop directly in the dung, without preparing any kind of underground nests. Lumaret & Stiernet (1989) stated that *A. obscurus* can occasionally behave as an endocoprid species, especially when large cattle dung pats are available: this is a further proof of the elevated adaptability of this species. The underground nesting behaviour of

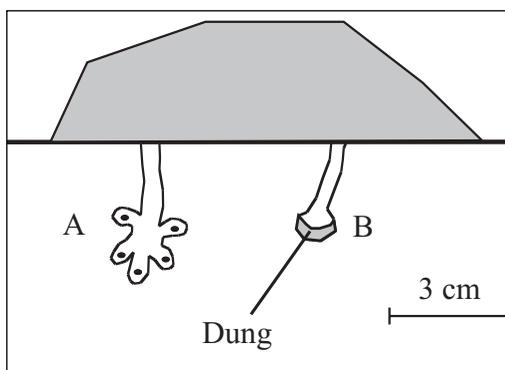


Fig. 2 - Nest of *Aphodius obscurus*. A.: deposition nest, with eggs; B.: development nest dug by the larvae.

A. obscurus which we were able to observe in the laboratory (Palestrini *et al.* 1997) must be considered an adaptation to the harsh climatic conditions of alpine habitats.

Aphodius (Ammonoecius) brevis (Erichson 1848)
Length 3.5-5 mm. Widely distributed in northern and central Europe, less common in the southern part of the continent, it reaches the Caucasus and Siberia. In Italy it is restricted to northern and central regions.

This species was collected only once, in cattle dung, near Grusiner (950 m) in the Orco valley.

Aphodius (s. str.) fimetarius (Linnaeus 1758)
Length 5-8 mm. Widespread in the Palearctic, introduced to North America and Australia. Known from most of Italy and the surrounding islands. In the GPNP it was collected up to 2600 m, but the highest densities are usually found below 1800 m. It prefers relatively aged dung (5-15 days from its deposition). It was observed in the dung of cattle, marmot, ibex, chamois and donkey. It is active from April to October, but the highest abundance is observed from mid-September onwards, when huge numbers of young individuals emerge from pupation and prepare themselves for hibernation.

Aphodius (Chilothorax) sticticus (Panzer 1798)
Length 4-5 mm. Distributed over most of Europe and Lesser Asia, the whole of Italy and its islands. This species usually favours sheltered habitats. In the study area we occasionally found this species in very high numbers (up to hundreds of individuals in a single dung pat), up to the altitude of about 1200 m. Highest densities are found in broad-leaved woods. *A. sticticus* is particularly abundant in late spring and early autumn. It was collected mostly in bovine, but on a few occasions we observed it also in wild boar dung.

Aphodius (Colobopterus) erraticus (Linnaeus 1758)
Length 5-7 mm. Widespread in Europe, except the most northern regions, North Africa, Siberia, Central Asia and northern China, introduced in North America. The Italian

range encompasses most of the peninsula and the surrounding isles, where it is usually found in well-exposed pastures. In our collections it reaches up to 2200 m in open and sunny habitats. We found it in various kinds of dung (ibex, goat, sheep), but a preference for cattle (59% of individuals collected) was evident. It is most abundant in the hottest part of the summer (July and August), at a time when several other species are temporarily rarer owing to increased environmental dryness. This ability to survive in drier conditions than those favoured by other species probably arises from the underground nesting behaviour of this species (Rojewsky, 1983; Zunino *et al.*, 1994), which enables the larvae to survive to the rapid parching of the dung left above the soil surface during hot spells.

Aphodius (Esymus) pusillus (Herbst 1789)

Length 3-5 mm. A common species in the Palearctic, known from most of Italy, Sicily and Sardinia. In the study area it was found in good numbers, mainly in open habitats up to 1800 m and during June and July. It was collected in cattle and ibex dung.

Aphodius (Oromus) alpinus (Scopoli 1763)

Length 5-6 mm. A species ranging over most of the mountain areas of central and southern Europe, from the Pyrenees up to the Carpathians. In Italy it occupies the entire Alpine arc. A typically alpine species.

We collected *A. alpinus* above 1800 and up to 2800 m, from late May up to August. After *A. obscurus*, it is the second commonest alpine species in the national park. It was found in several kinds of dung (ibex, sheep, cattle, more rarely chamois and marmot). Preliminary observations in the laboratory suggest that this species has perhaps some interesting adaptations to the alpine habitats, such as underground egg deposition and rapid larval development.

Aphodius (Otophorus) haemorrhoidalis (Linnaeus 1758)

Length 4-5 mm. An Holarctic species, known

from the whole of Italy and the principal isles. We collected it up to 2000 m during summer. *A. haemorrhoidalis* is a quite common and widespread species, but it is rarely numerous. It was always collected in cattle dung.

Aphodius (Parammoecius) corvinus (Erichson 1848)

Length 3-4 mm. A mostly central European species, known in Italy from the western Alps and the Apennines up to the Sila, usually found in sheltered habitats at medium or high altitudes.

In the GPNP this species is common from May to September, from 1400 to 2300 m, in cattle (63% of individuals) and ibex (37%) dung; in a few occasions it was also found in chamois dung. *A. corvinus* has a very clear preference for wooded, both conifer and broad-leaved, habitats, where 86% of individuals were collected.

Aphodius (Parammoecius) pyraeneus

(J. Du Val & Fairmaire 1859)

Length 4-5 mm. Unevenly distributed in alpine localities of south-western Europe, mainly in the Pyrenees and the western Alps, also known from one locality in the northern Apennines.

This is a normally rare species, but in the study area we collected it quite frequently, at high altitudes (2400-2800 m), in July and August. Most of the individuals (85% in our collections) were collected in Marmot dung found near the entrance of their underground shelters; perhaps, this suggests an explanation for the alleged rarity of this beetle, since marmot dung, being usually deposited in underground latrines, is probably rarely inspected by entomologists.

A. pyraeneus was also found in ibex and chamois dung, but almost always at sheltered sites, such as the resting places of wild ungulates. We believe that the interesting ecology of this species could not be a consequence of a very narrow food selection (i.e. marmot dung), but, as an adaptation to high altitude habitats, of a strong preference for sheltered microhabitats with favourable

microclimates, such as dens and dormitories of wild mammals.

Aphodius (Planolinus) borealis (Gyllenhal 1827)
Length 3-4 mm. An Holarctic species, usually found in montane habitats in the southern part of its range. Known from most of Italy and the largest isles.

In our collections this species is usually common or very abundant from May to October. It was collected in cattle, chamois and ibex dung, up to 1800 m, and showed a clear preference for woody habitats.

Aphodius (Planolinus) fasciatus (Olivier 1789)
(=*uliginosus* (Hardy, 1847))

Length 3.5-4.5 mm. A widely ranging species in the Holarctic region, found in northern and central Italy, up to Tuscany, with a preference for sheltered habitats.

In our collection this is a scarcely represented species, usually found in late summer or early autumn up to 1500 m of altitude.

Aphodius (Teuchestes) fossor (Linnaeus 1758)
Length 10-13 mm. An Holarctic species, ranging over most of the Italian peninsula, favouring medium altitude, well-exposed pastures. We found this species up to about 1800 m, during most of the summer, in open habitats and mostly in cattle dung. *A. fossor* has a paracoprid nesting behaviour: adults dig short underground galleries ending with chambers where a small amount of dung is brought from the surface and one egg is laid; most, but probably not all, of the larval development takes place in these chambers (Zunino & Barbero, 1990).

Euheptaulacus carinatus (Germar 1824)

Length 4-6 mm. A species ranging over the montane areas of central and southern Europe, Palestine, Caucasus, eastern Siberia and northern China, in Italy known from the western Alps, central and southern Apennines and Sicily. This is usually a species of well exposed mountain pastures.

In our study area we found it, sometimes in

abundance, in pastures over 2000 m, but only during a short time spell of about one month, between July and August, during the hottest part of the summer period.

Family Scarabaeidae

Onthophagus (s. str.) illyricus (Scopoli 1763)

Length 6-11.5 mm. The range of this species covers most of southern and central Europe, Syria, Iran and Lesser Asia.

We collected this species on only one occasion, in the medium Orco valley (Rosone), at the altitude of 715 m, in cattle dung. The locality of collection is outside the national park, but nevertheless very near to its border.

Onthophagus (s. str.) taurus (Schreber 1759)

Length 6-11.5 mm. A species found in central and southern Europe, North Africa, Lesser Asia, Palestine and the Middle East. It ranges over most of the Italian territory.

We collected this species up to about 1000 m in June and July, usually in bovine, only rarely in sheep dung.

Onthophagus (Palaeonthophagus) joannae (Goljan 1953)

Length 4-6 mm. Distributed in Spain, France and the Balkans. In Italy it occupies the whole of the peninsular area. An orophile species, typical of mean altitude localities, especially in the southern part of its range.

In the GPNP, this small sized *Onthophagus* is very common up to 1000 m. It mostly chooses open habitats, but feeds on several kinds of dung (cattle, man, wild boar, sheep, ibex)

Onthophagus (Palaeonthophagus) baraudi (Nicolas 1964)

Length 5-6 mm. An endemic species of the western Alps, *O. baraudi* is typical of high altitude habitats, and prefers well exposed locations.

This species was collected in cattle and ibex dung in May 1997 at a few nearby localities, in the northern section of the national park (Valnontey, 1700 m, Rifugio Sella, 2500 m).

Onthophagus (Palaeonthophagus) fracticornis (Preysslér 1790)

Length 7-10 mm. A species with Euroturanic distribution, mainly found in montane areas in the southern part of its range. In Italy it is known from all the peninsular region.

O. fracticornis is by far the commonest Scarabaeid beetle of montane and alpine habitats. It was collected up to 2700 m, in ibex, sheep and cattle dung. It usually reaches the highest densities below 1800 m. It is common from May to October, and especially in early autumn, when young individuals, born in the preceeding summer, complete their larval development and undergo a maturation period which precedes hibernation.

Onthophagus (Palaeonthophagus) coenobita (Herbst, 1783)

Length 6-10 mm. This beetle is found over most of Europe, except the northern most areas.

O. coenobita was collected in cattle dung at Rosone, in the Orco valley, at about 750m. Although the collection site lies slightly outside the borders of the national park, it is possible that future research will locate it inside the protected area.

4. Discussion

During this survey we collected 27 species of coprophagous Scarabaeoidea within the area of the GPNP; three more species (*G. mutator*, *O. illyricus*, *O. coenobita*) were collected outside, but very near to, the borders of the protected area.

Aphodiidae are clearly the dominant taxa (20 species, 67% of the total), while Geotrupidae (4 species, 13%) Scarabaeidae (6 species, 20%). A detailed analysis of the number of individuals collected will be carried out in later works, but the dominance of the Aphodiidae seems to be even more marked if the number of individuals is considered. This result was not unexpected, as Aphodiidae are known to be the dominant group of alpine and northern communities (Barbero *et al.*, 1994; Lumaret &

Stiernet, 1991, 1992).

The dung beetle fauna of the GPNP is rich and diverse, and this confirms our hypothesis that an abundant presence of mammalian herbivores should determine an equally rich coprophagous fauna. The insect community which we studied seems to be well adapted to montane and alpine environments and exploits a wide range of the available food resources.

All the kinds of herbivore dung found in the national park are occupied by one or more dung beetle species. Several taxa are quite euriecious, but a few clear preferences were highlighted, such as that of *A. scybalarius* for cattle dung. The most obvious example is the partiality of *A. pyraeneus* for marmot dung.

As for the two main herbivore species in the national park, ibex and chamois, we have usually noticed a higher presence of beetles, both in the number of species and in that of individuals, in the dung of the former than in that of the latter. This seems to be a consequence of the smaller size of chamois' dung, which is therefore much more subject to climatic factors, to parchement in particular, which can rapidly make them unsuitable to the survival of the insects.

Coming to habitat selection, the differences between the species are usually well marked. At higher altitudes the dung community is dominated by a small number of taxa, having their maximum densities above 2000 m, such as *Aphodius obscurus*, *A. alpinus*, *A. pyraeneus*, *A. satyrus* and *Euheptaulacus carinatus*. Under 2000 m, clear differences exist between open and wooded habitats.

In the pastures, species like *Aphodius erraticus*, *A. fossor*, *A. fimetarius*, *A. scybalarius*, *A. pusillus*, *Onthophagus fracticornis* are common. In the woods, the dominant species are instead *A. corvinus* (above 1400 m), *A. sticticus* (under 1200 m) and *A. borealis*. Some species, such as the Geotrupidae, *A. rufipes* and *A. depressus* can be found both in wooded and in open habitats. Finally it should be noted that, during the hottest part of the

summer, some species (*A. rufipes*, *A. depressus*) temporarily leave the open pastures and appear with higher frequencies inside the more sheltered woodland habitats. This seasonal shift must be considered a consequence of temporary arid conditions arising in open habitats during summer.

As for reproductive biology, we showed that a strikingly high number of species in the genus *Aphodius* (*A. obscurus*, *A. scybalarius*, *A. alpinus*, *A. fossor*, *A. erraticus*, *A. ater*) have underground nesting behaviour and larval development. This is relatively rare within the genus (Cambefort & Hanski, 1991). We hypothesise that these behaviours are probably explained as an adaptation to extreme climatic conditions (summer aridity, high levels of solar radiation, wide temperature fluctuations) often met in alpine environments.

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References

- BARAUD J. (1992). *Faune de France. France et régions limitrophes*. 78. Coléoptères Scarabaeoidea d'Europe. Soc. Linn. Lyon, 856 pp.
- BARBERO E., PALESTRINI C. & ZUCHELLI M. (1994). Il popolamento di Scarabaeoidea coprofagi (Insecta: Coleoptera) del Parco Naturale del Monte Avic (Valle d'Aosta, Italia). *Rev. Valdôtaine Hist. Nat.*, 48: 5-28.
- BISTRÖM O., SILFVERBERG H. & RUTANEN I. (1991). Abundance and distribution of coprophilous Histerini (Histeridae) and *Onthophagus* and *Aphodius* (Scarabaeidae) in Finland (Coleoptera). *Ent. Fenn.*, 27: 53-66.
- CAMBEFORT Y. & HANSKI I. (1991). Dung beetle population biology. In: Hanski I., Cambefort Y., (Eds.). *Dung Beetle Ecology*. Princeton University Press, Princeton, pp. 36-50.
- DE BIAGGI E., STOPPA T. & SCOTTA M. (1990). Proposta per una suddivisione del Piemonte in settori eco-geografici. *Riv. Piem. St. Nat.*, 11: 3-40.
- DELLACASA G. (1983). *Sistematica e nomenclatura degli Aphodiini italiani (Coleoptera, Scarabaeidae, Aphodiinae)*. Monogr. Mus. Reg. Sci. Nat. Torino 1: 1-465.
- HALFFTER G. & MATTHEWS E. G. (1966). The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera: Scarabaeidae). *Fol. Entomol. Mex.* 12-14: 1-312.
- LUMARET J. P. (1990). *Atlas des Coléoptères Scarabaeides Laparosticti de France (Inventaire de Faune et de Flore, Fascicule 1)*. Secrétariat de la Faune et de la Flore, Muséum National d'Histoire Naturelle, Paris.
- LUMARET J. P. & STIERNET N. (1989). Inventaire et distribution des Coléoptères Scarabaeides coprophages dans le massif de la Vanoise. *Trav. Sci. Parc Nation. Vanoise*, 18:193-228.
- LUMARET J. P. & STIERNET N. (1991). Montane dung beetles. In: Hanski, I., Cambefort, Y., (Eds.). *Dung Beetle Ecology*. Princeton University Press, Princeton, pp. 242-254.
- LUMARET J. P. & STIERNET N. (1992). Biogeography of dung beetle communities in the western and central Alps (Coleoptera, Scarabaeoidea). *Biogeographia*, 16: 425-436
- PALESTRINI C., BORGHESIO L. & BARBERO E. (1997). A new pattern of nesting behaviour in the genus *Aphodius* (Coleoptera, Scarabaeoidea). *Advances in Ethology*, 32: 303.
- PIGNATTI, S. (1976). Geobotanica. In: Cappelletti C. (Ed.) *Trattato di Botanica*. UTET, Torino.
- ROJEWSKY C. (1983). Observations on the nesting behaviour of *Aphodius erraticus* L. (Coleoptera, Scarabaeidae). *Polsk. Pism. Ent.* 53: 271-279.
- ZUNINO M. & BARBERO E. (1990). Food relocation and the reproductive biology of *Aphodius fossor* (L.) (Coleoptera Scarabaeidae Aphodiinae). *Ecol. Ethol. & Evol.*, 2: 334.
- ZUNINO M., CANINO L. & COLETTA E. (1994). Feeding and nesting behaviour of *Aphodius (Colobopteris) erraticus* (L.) (Coleoptera Scarabaeidae Aphodiinae). *Ecol. Ethol. & Evol.*, 6: 451-452.