Diversity and ecological role of dung beetles in Iberian grassland biomes

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Dung beetles play a major ecological role in pastures through breaking-down livestock faeces, draining soils and aiding recycling of organic matter and nutrients. Consequently, pasture quality and productivity depends on the activity of these beetles. In addition, any changes to the dung beetle community structure might have an effect on the vertebrate fauna of an area, since the beetles are important prey items for many bats, reptiles, birds and mammals. This paper therefore emphasises that a sound understanding of the ecological role played by dung beetles is essential for the management, conservation and maintenance of traditional Mediterranean livestock grazing systems.

Los escarabajos del estiércol juegan un papel ecológico importante en los pastos deshaciendo las heces del ganado, secando el terreno y ayudando a reciclar las materias orgánicas y nutrientes. Consecuentemente, la cantidad de pasto y productividad depende de la actividad de estos escarabajos. Además, cualquier cambio en la estructura de los escarabajos del estiércol puede tener un efecto en los animales vertebrados de un área, debido a la importancia de los escarabajos como presa para muchos murciélagos, reptiles, aves y mamíferos. Esta ponencia, por eso, enfatiza que un buen entendimiento del papel ecológico jugado por los escarabajos del estiércol es esencial para el control, conservación y mantenimiento de los sistemas tradicionales de ganadería mediterráneos.

Les bousiers jouent un rôle écologique important dans les pâturages en décomposant les excréments du bétail, en drainant les sols et en facilitant le recyclage des substances nutritives et des matières organiques. Par conséquent, la qualité et la productivité des pâturages dépendent de l'activité de ces scarabées. En outre, toute modification de la structure de la communauté de bousiers peut avoir des répercussions sur la faune vertébrée d'une zone car les scarabées sont d'importantes proies pour un grand nombre de chauves-souris, reptiles, oiseaux et mammifères. Ce document souligne donc qu'une bonne compréhension du rôle écologique joué par les bousiers est essentielle à la gestion, à la conservation et au maintien des systèmes de pacage traditionnels méditerranéens.

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Introduction

Insect communities inhabiting the faeces of large mammals are surprisingly rich and diverse. A single site can be colonised by more than 200 coprophilous species (Hanski 1987), belonging to different families of Coleoptera (Scarabaeidae, Geotrupidae, Aphodiidae, Hydrophilidae, Staphylinidae and Histeridae) and Diptera (Muscidae, Calliphoridae, Sarcophagidae, Sepsidae and Sphaeroceridae.

However, dung beetles (Scarabaeoidea: Scarabaeidae, Geotrupidae and Aphodiidae) are the main biological agents of dung decay in grassland biomes in the West-Palaearctic region (Ridsdill-Smith & Kirk 1981). The warmer the environmental conditions, the more ecologically important dung beetles are. Therefore, dung-associated beetles play a more important ecological role in southern Europe than they do in northern Europe (Hanski 1986), and also are more important during spring and summer than in autumn and winter. So much so that in the Iberian Peninsula dung beetles comprise between 65% and 90% of the total biomass in each dung pat (Lobo

1991).

Dung beetles are very diverse (nearly 8,500 species) and are well adapted to life in the faeces of large herbivores in grassland biomes. Habitat requirements and colonisation abilities seem to have been selected for many times during the past two million years. Therefore, the present dung beetle communities were probably pre-adapted to grassland biomes. In the majority of species, both adults and larvae feed exclusively on dung. Many of them show complex feeding and nesting behavioural patterns (such as food relocation, parental care) which reduce competition for resources (Halffter & Edmonds 1982).

The coprophilous community is a true trophic network basically maintained by an intermittent energy source distributed in ephemeral units which are isolated one from another (i.e. the dung pats). Ephemerality and discreteness (essential ecological features of dung resource) best define this microhabitat, determining the most striking adaptation of dung-associated communities - their dispersal capacity. For example, it has been observed that some *Onthophagus* species are able to disperse 350 m per day, while introduced dung beetles have dispersal rates which range from 50 km to 130 km per year (e.g. Barbero & López 1992; Hanski & Cambefort 1991a). This dispersal rate would allow the crossing of the Iberian Peninsula in 10-20 years.

The Iberian Peninsula contains more than 200 dung beetle species (Veiga & Martín-Piera 1988). However, a single dung pat from any site can provide a good representation of the local fauna at any time, and any local fauna can also provide a good representation of the regional fauna. For example, a region of 100 km^2 may contain nearly 60 species, any grassland of 100 m^2 may contain more than 40 species, and a single dung pat will easily provides a collection of 15 to 20 species (Lobo 1992a; Lobo & Martín-Piera 1994; Martín-Piera, Veiga & Lobo 1993).

Although high dung beetle dispersal rates could have led to observations of high local community diversities, another ecological feature might also be a determining factor - the production rate of dung pats cannot be influenced by dung beetles communities. This means that the level (quantity) of microhabitat resources depends mainly on external factors. Hence, the consumer-producer relationship is uncomplicated by coevolution feedback. The dung microcosm is a true subsystem linked with (and depending on) the more expansive grassland ecosystem. The lack of consumer-resource production rate feedback may have increased the role of competition within these communities (Hanski 1987; Hanski & Cambefort 1991b). Therefore competition might enhance, and may help us to explain, observations of high levels of diversity.

Nutrient cycling

Although dung production rate does not depend on dung beetle activity, a certain number of studies have largely proved that plant yield biomass, quality and palatability of pastures do increase with dung-associated beetle activity (e.g. Bornemissza 1976; Gillard 1967; Fincher 1981; Rougon *et al.* 1988). In other words, while coprophagous communities may form only a subsystem, they also make a major contribution to the performance of the grassland ecosystem to which they are linked and dependent upon.

Data available from the northern latitudes of temperate biomes indicate that dung beetles neither dry nor remove mammal faeces (Stevenson & Dindal 1987). Dung beetle food intake efficiency in these latitudes is generally lower than that of other herbivorous insects (Holter 1974). This low general efficiency appears to be compensated for by a large daily food intake, ranging from 150% to 400% in the only well known case (*Aphodius rufipes*: Holter 1974). This means that a normal population of 100 beetles per dung pat can ingest 334 g of dung in five days (Holter 1979).

However, in southern latitudes the food intake efficiency of Scarabaeidae seems to be very high (Myrcha 1973). Moreover, dung dispersal capacity is also very high - a single nesting pair of *Copris lunaris* (2 beetles = 1.13 g live weight) is able to bury between 75g and 140 g of dung per day (Myrcha 1973). These figures are substantially higher with some other species, e.g. *Heliocopris japetus* can bury 3 kg of dung in a single breeding burrow (Klemperer & Boulton 1976). Among Scarabaeidae, the ratio of beetle live weight to mass of dung removed ranges between 1:5 and 1:1000 (Doube 1990).

Although there is not much information from the Iberian Peninsula, some estimates suggest that dung removal rate can reach 80% (Ridsdill-Smith & Kirk 1981) and that the faeces weight loss due to dung beetle activity ranges from 9% to 25% (Lobo 1991). The Iberian Peninsula climate allows dung beetles to be active throughout almost all the year. Furthermore, if we take into account the long-established tradition of livestock grazing, the recent underuse of some pastures (Montoya 1983) and the increase in intensive grazing on others (Fillat & Montserrat 1981), then it

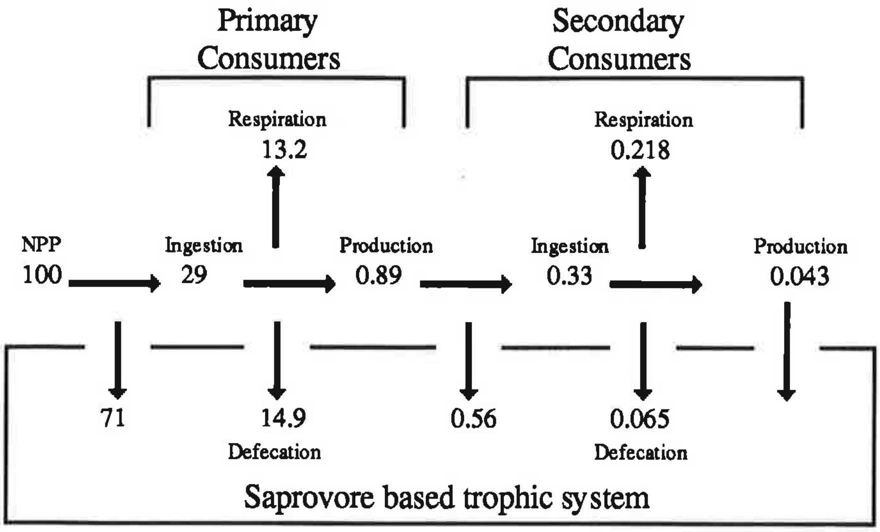

Figure 1. Energy flow in a pasture ecosystem (Kcal per m^2 per year) after Heal & MacLean (1975). NPP = Net Primary Production.

would appear to be essential to know the ecological role of the dung beetle fauna in nutrient cycling on Iberian grassland biomes.

The decay of faeces from large herbivores plays a major ecological role in recirculation of energy, organic matter and nutrients (Heal & MacLean 1975). Dung-associated beetles inhabiting Mediterranean grassland ecosystems strengthen this ecological role because they are the main biological agents which remove and mineralise the dung. As Figure 1 shows, 14.9% of the pasture Net Primary Production goes into the decomposer trophic system through large herbivores excreting nearly 50% of the energy they ingest. Assuming that some 15% of that energy is ingested by the coprophagous fauna, and estimating assimilation efficiency to be around 20%, we obtain a production of 0.45 Kcal/m^2/year (a figure 10 times higher than that of secondary consumers and equivalent to half of the primary consumer's production).

It is essential that complete studies on this subject are conducted in the Iberian Peninsula as soon as possible. We can, however, obtain a preliminary estimate from the following example:

> In a one hectare pasture, two cows who each produce 12 dung pats per day (McKinney & Morley 1975) would together produce a total of 720 dung pats over a 30 day period, i.e. a total fresh weight of dung of 1,800 kg (Sainz & Compaire 1985).

If we consider that migration (rather than immigration) becomes dominant after the fifth day after dung deposition (Lobo 1992b), we can estimate that only 120 dung pats contain abundant populations (2 cows x 12 dung pats/day x 5 days).

Taking into account our previous estimates (3,000 beetles/kg dung), that means that a single hectare may be colonised by nearly 360,000 beetles (which is equivalent to 2,040 g of dry weight biomass or some 7 kg of fresh weight biomass).

Now, if we also take into account the fact that nitrogen makes up 2% of dry weight of dung, and that the activity of dung-associated beetles decreases the amount of nitrogen released to the atmosphere by 15% (Gillard 1967), we can infer that the activity of coprophilous beetles might incorporate some 0.7 kg of nitrogen per ha per month into the soil. Over a 180 day grazing period, this would result in a total of 4.2 kg per ha (i.e. one sixth of the amount of nitrogen required to manure a pasture: Selke 1968).

Dung beetles and higher trophic levels

Dung beetles can also accelerate nutrient cycling and the energy flux in other trophic levels of grassland ecosystems.

Dung beetle/predator biomass proportions reaches 3/1 or 4/1 in northern Europe (Hanski & Koskela 1977) and 2/1 in central Europe (Desière 1987). These figures are quite similar to those obtained by Schwarz (1975) for the relationship between primary and secondary consumers. Equivalent figures have also been obtained in the Iberian Peninsula for the autumn and winter months, but in spring (when dung beetle colonisation is at its highest) there is a marked increase in these figures to between 7/1 and 19/1 (Lobo 1992b).

Flies are considered to be the only coprophilous insects which appear to be intensively predated (e.g. Koskela & Hanski 1977; Fay & Doube, 1983). That is why predation has been has been considered to be the main force structuring Dipteran communities (e.g. Hanski 1987; Koskela & Hanski 1982). However, dung beetles appear to be more intensively predated by vertebrate predators.

Very few papers have been published about the importance of dung as a source of invertebrate food for vertebrates. Kingston & Coe (1977) suggested that predation is the selective pressure which determines burying depth in the African *Heliocopris* spp., and Lobo (1992b) and Cambefort (1991) have also speculated that colour patterns and immobilisation reflex might be defensive adaptations. Cow dung also appear to be an important source of food for the chough *Pyrrhocorax pyrrhocorax* throughout its European range (e.g. Bignal & Curtis 1989; McCracken & Foster 1994; McCracken *et al.* 1992). At least the two first waves of successive invasions colonising dung are potentially useful prey for that bird - Diptera (the larger Stratiomyidae, Muscidae and Scatophagidae larvae) and Coleoptera (adults and larvae of the larger Staphylinidae and Scarabaeoidea beetles). We have often identified abundant fragments of *Geotrupes* spp. and other non-coprophagous Scarabaeoidea (such as *Rhizotrogus* spp.) in fox dung, especially in the autumn.

It has been suggested that the abandonment of mountain grazing, as well as the substitution of some types of domestic livestock for others (sheep for cattle and goats for horses) deprives the chough of beetles and others insects which colonise the dung of cattle and horses (García 1989). While the effect of abandonment seems self evident, some consideration should be given to the effect of substitution.

Dung beetles, having evolved over a long time period to cope with ungulate dung, are able to react quickly and easily to sudden changes in dung type. The guild diversity and the complexity of reactions among native species have made these communities highly adaptable to change (Lumaret, Kadiri & Bertrand 1992). The only changes detected by these authors concerned the relative frequencies of many species (mainly with regard to biomass), and qualitative differences were restricted to six non-abundant species. The remaining 37 species from a total of 43 were common to both sheep and cattle dung in the same place. It should be immediately emphasised that the changes in grazing regime studied by Lumaret, Kadiri & Bertrand (1992), were the inverse of that mentioned by Garcia (1989).

Effects of veterinary antiparasitic drugs

In the last decade, much attention has also been paid to the effects of residues of the veterinary antiparasitic drug ivermectin on coprophilous insects. Avermectin residues in cattle and sheep dung have been implicated in a variety of lethal and sublethal effects in a range of dung-associated insects (e.g. McCracken & Foster 1993; Lumaret *et al.* 1993; Wardhaugh *et al.* 1993). These include acute toxicity to the adult and larval stages of dung-feeding Diptera and Coleoptera, as well as a range of sublethal effects (such as abnormal feeding, reduced fat accumulation, delayed reproduction and impaired mating performance).

Differences in the apparent toxicity of sheep and cattle dung following ivermectin treatment are evident. For example, ivermectin residues in sheep dung have important deleterious effects on the survival, fecundity and reproductive development of *Euoniticellus fulvus* adult beetles, but these were much less marked than those recorded in cattle dung (Wardhaugh *et al.* 1993). These authors suggest that the effects of ivermectin-contaminated sheep dung are certain to be much more transient than those associated with the dung of treated cattle, and that this is so because sheep dung is a much more ephemeral resource than cattle dung.

Summarising all presently available results show that the potential environmental impact of ivermectin is variable and correlates with multiple factors, mainly:

Local, regional, and probably even seasonal climatic conditions.

Structure, water content, volume and ephemerality of different dung types.

Dung-feeding species.

It has also been suggested that ivermectin residues in dung could potentially have adverse effects on populations of the chough (and other wildife species) by affecting potential prey items (McCracken 1993). However, detailed research needs to be conducted at different sites and with different coprophilous communities before the true environmental impact of antiparasitic veterinary livestock drugs on vertebrate predators can be assessed.

Conclusions

Dung beetles communities inhabiting the faeces of large mammals form a subsystem linked to and dependent on grassland ecosystems. Therefore, the abandonment of grazing livestock might produce a parallel decrease in the coprophagous insect fauna. Dung-associated beetle activity cannot increase production of the resource. However, the relatively recent introduction of domestic livestock to Australia (where there are no native coprophilous insects which can cope with large dung pats) has underlined the fact that the dung microcosm performs a major influence on pasture ecosystems.

Although dung beetle dispersal capacity has not been studied in detail, it is commonly assumed that this adaptation to the resource ephemerality enables them to rapidly colonise any territories colonised by wild and domestic herbivores. However, many important questions still remain, such as:

When livestock move from one site to another, how long does it take before colonisation by the dung beetle fauna occurs?

What are the characteristics of that colonisation?

For how long is mineralisation and nutrient cycling delayed?

The answers to all these questions would allow us to predict the effects of current changes in grazing regimes, and would also provide us with a better understanding of dung beetle diversity in Iberia.

Since the 1950s, changes to grazing regimes have resulted in dramatic reductions in cattle, sheep and goat numbers in the Mediterranean region, and hence the availability of dung to beetles has been reduced. Fortunately, pastoral practices are still practiced in a few Mediterranean pasture ecosystems (such as transhumance in the mountains and livestock grazing in the wooded dehesas), and consequently dung beetle populations have been maintained. However, a sound understanding of the ecological role played by dung beetles is essential for the future management, conservation and maintenance of traditional Mediterranean livestock grazing systems.

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