



Regional and local influence of grazing activity on the diversity of a semi-arid dung beetle community

Jorge M. Lobo,* Joaquín Hortal and Francisco J. Cabrero-Sañudo

Departamento de Biodiversidad y Biología Evolutiva, Museo Nacional de Ciencias Naturales, C/José Gutiérrez Abascal, 2 28006 Madrid, Spain

ABSTRACT

This study analyses the effect of resource availability (i.e. sheep dung) on dung beetle communities in an arid region of Central Spain, both at regional and at local scales. A total of 18 sites within 600 km² were sampled for the regional analysis and 16 sites within the 30 km² of an Iberian municipality were sampled for the local analysis. Spatial and environmental characteristics of sampling sites were also compiled at both scales, including measures of grazing activity (livestock density at regional scale, and two counts of rabbit and sheep dung at local scale). At a regional scale, any environmental or spatial variable can help to explain the variation in abundance. However, species richness was related to summer precipitation and composition was related to elevation. At local scale, abundance is not significantly related to any of the environmental variables, but species richness was related to the local amount of sheep dung (27% of variance). The amount of dung in a 2-km buffer around the site accounts for 27–32% of variance in abundance and 60–65% of variance in species richness. The presence of the flock with the highest sheep density explains 53% of abundance variability and 73% of species richness variance. A cluster analysis of localities identified two main groups, one characterized by a lower abundance and species richness that can be considered a nested subsample of the species-rich group. The mean and maximum amount of sheep dung in the sites separated by less than 2 km are the only significant explanatory variables able to discriminate both groups.

These results suggest that grazing intensity (and the associated increase in the amount of trophic resources) is a key factor in determining local variation in the diversity and composition of dung beetle assemblages. However, dung beetle assemblages are not spatially independent at the analysed resolution, and the amount of dung in the surroundings seems to be more important for locally collected species than the dung effectively found in the site. Although differences in the availability and quantity of trophic resources among nearby sites could be affecting the population dynamics and dispersion of dung beetles within a locality, sites with larger populations, and greater species numbers would not be able to exercise enough influence as to bring about a complete local faunistic homogenization.

Keywords

Resource availability, Scarabaeidae, semi-arid ecosystems, sheep grazing activity, species richness determinants.

*Correspondence: Jorge M. Lobo, Departamento de Biodiversidad y Biología Evolutiva, Museo Nacional de Ciencias Naturales, C/José Gutiérrez Abascal, 2. 28006. Madrid, Spain. Tel.: 34 +91 4111328. Fax: 34 +91 +5645078. E-mail: mcnj117@mncn.csic.es

INTRODUCTION

Dung beetles are a highly specialized trophic group mainly adapted to the consumption of herbivore dung (Cambefort, 1991). In extensive cattle systems, transformed plant material (such as livestock dung) constitutes the greatest source of nutrients (Andrzejewska & Gyllenberg, 1980). Thus, dung beetles play a key role in nutrient cycles of grazed pasturelands (see, e.g.

Fry & Lonsdale, 1991 or Martín-Piera & Lobo, 1995), so their absence produces critical changes in ecosystem functioning (see, e.g. Gittings *et al.*, 1994). Although cattle movement effectively redistributes nutrients in dung-rich situations (Gómez Sal *et al.*, 1992), the probability of nutrient loss from the system is remarkable, and pronounced nutrient cycles would be strongly influenced by the high consumption and low assimilation rates of dung beetles (Holter, 1975, 1982). In traditionally managed

landscapes in Europe, the interactions among livestock, grazing, vegetation structure and dung beetles constitute a complex system (Roslin & Koivunen, 2001). Both the amount of dung available and the vegetation structure are a consequence of grazing intensity and/or abundance of herbivores; thus, changes in their management (e.g. livestock herding abandonment) also strongly affect the associated dung beetle fauna (see, e.g. Verdú *et al.*, 2000 or Hutton & Giller, 2003). Therefore, measurement of the response of dung beetle assemblages to livestock changes is crucial for managing the plant–herbivore–coprophagous system correctly. For instance, when extensive cattle grazing began in regions such as Australia or North America, where the local dung beetle fauna were unable to consume the excrements produced, major ecological alterations occurred that had to be overcome by the introduction of Mediterranean and African dung beetles (Bornemissza, 1976; Fincher, 1981).

Unlike the case in other regions, in the west Palaearctic temperate region, most dung beetle species seem to have only slightly significant dung type preferences (Martín-Piera & Lobo, 1996; Gittings & Giller, 1998), only differing in their relative abundance across dung types (Finn & Giller, 2002). However, if the variety of trophic resources does not seem to be a determining factor the relevance of dung quantity (i.e. food availability), a factor closely related (more herbivore species can imply a higher quantity of dung), is rarely considered to explain the diversity and composition of dung beetle assemblages. It is known that these assemblages seem to be able to rapidly readjust their populations to the level of available trophic resources, both in grasslands (Lumaret *et al.*, 1992) and in forests (Kadiri *et al.*, 1997); and that they also react quickly to the changes in the type of ruminants and the cattle activity history (Lumaret *et al.*, 1992; Lobo *et al.*, 1998). However, we ignore which is the local response to the regional heterogeneity in the quantity of resources, and which are the colonization capacity and the spatial extent of influence of these local assemblages. Knowing these questions can help to determine the capacity of restoring these communities after the changes in cattle uses occurred in the last decades, and the verified decline of some species (Lumaret, 1990; Biström *et al.*, 1991; Barbero *et al.*, 1999; Lobo, 2001; Pitkänen & Roslin, 2001; Roslin & Koivunen, 2001; Hutton & Giller, 2003). In the Iberian Peninsula, agricultural and cattle-herding activities over long periods of time have created highly productive and complex landscapes where intermediate perturbation levels propitiated by human activity maintain high biological diversity (species richness and replacement, habitat diversity, etc.; see Bernáldez, 1992; Gómez Sal *et al.*, 1992; Beaufoy *et al.*, 1995). Unfortunately, the replacement of traditional cattle-herding practices by other more profitable ones that require the importation of forage is sparking also a change in cattle landscapes (Ruiz & Ruiz Pérez, 1984; Bernáldez, 1991). This effect should be crucial in Mediterranean semi-arid regions, where extensive cattle-herding practices have allowed the development of a sustainable economy in low productive areas during the former centuries.

Dung beetle species frequently show strong intraspecific aggregation patterns, decreasing the interspecific aggregation with the increasing of patch size (Hutton & Giller, 2004). This

aggregation is probably the consequence of the high rate of movement among individual pats within the same pasture, and the concomitant low rate of between pasture movements (Roslin, 2000). This spatial pattern probably generated by behavioural mechanisms would hinder the regional homogeneity of these assemblages in spite of the supposedly high capacity of dispersion of species like these, adapted to ephemeral habitats, and their great capacity of reaction to the local changes in resources. However, as the dispersal power and the level of spatial aggregation vary among species (Roslin & Koivunen, 2001), local composition and richness would depend on the level of resources in the surrounding localities, whilst regional composition and richness would depend on the degree of local differences in resources and their history of cattle changes.

Sampling dung beetle assemblages of a semi-arid region (less than 500 mm year⁻¹ of precipitation) of central Iberian Peninsula characterized by a low availability of trophic resources, this paper aims to study the regional and local variations in the species richness and the faunistic composition of these communities according to sheep grazing, habitat structure and environmental factors. The objective is to estimate at which extent dung beetle assemblages depend on the quantity of available resources in each locality and in surrounding localities.

METHODS

Study area

Two sampling campaigns were carried out, one to describe regional composition and geographical variations in dung beetle assemblages and the other to characterize local variations between close sites due to differences in grazing intensity.

The regional sampling was accomplished around the south-eastern borders of the Comunidad de Madrid (Central Spain), comprising nearly 600 km² of a semi-arid region dominated by sedimentary gypsum soils with moorlands in the valleys. The altitude of this territory oscillates approximately between 470 and 670 m a.s.l., with annual precipitation scores between 410 mm and 470 mm, and mean annual temperatures between 12.5 and 14.5 °C, approximately. These kind of semi-arid environmental conditions generate a shrub–steppe landscape relatively frequent in the Iberian Peninsula (see map at Fig. 1), compositionally related to similar landscapes present in Central Asia and North Africa, which expanded from the Irano–Turanian region through the Mediterranean basin during the Tertiary (Suarez Cardona *et al.*, 1992). In most Iberian steppes, the semi-arid climate and the prevalence of sheep livestock yield poor dung beetle assemblages (see Hortal-Muñoz *et al.*, 2000; Sánchez-Piñero & Ávila, 2004), specialized to the consumption of a much more ephemeral and scarcer resource. Under such conditions, the response of dung beetles to changes in resource availability should be rapid. Thus, these habitats seem the most appropriate to study the influence of trophic resources quantity in Iberian dung beetle assemblages. Accordingly, the region is grazed basically by sheep and goats, with some cow herds generally relegated to the valleys with more sedimentary soils and

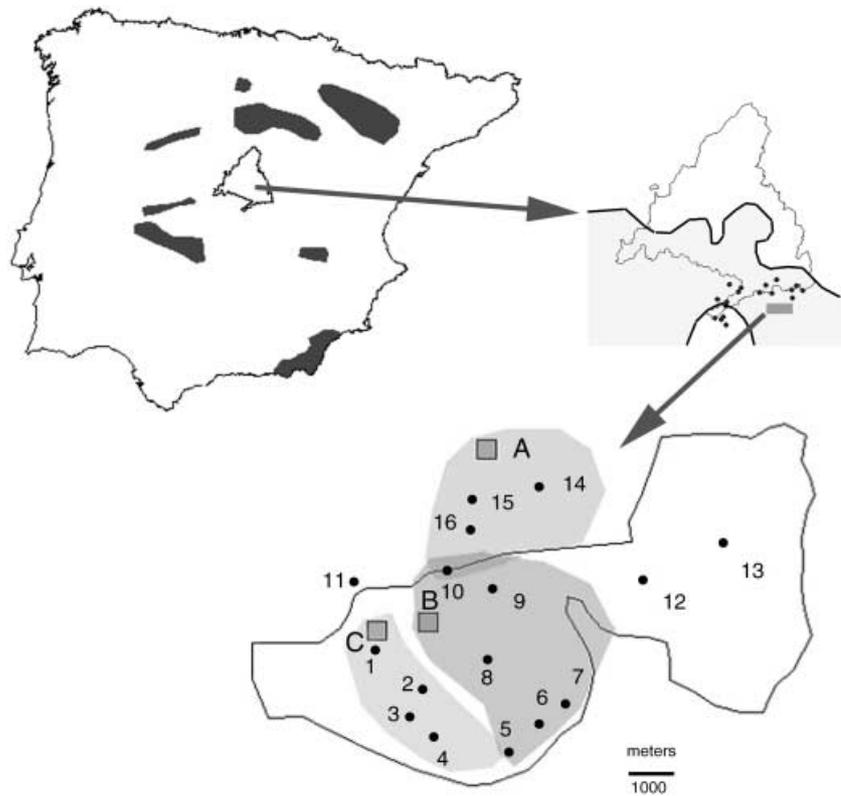


Figure 1 Location of the Comunidad de Madrid and approximate geographical situation of semi-arid regions within the Iberian Peninsula (black areas; see Suarez Cardona *et al.*, 1992). The location of the 18 localities used for the regional sampling is showed on the right, where the local sampling area (grey rectangle) and the area with summer precipitations lower than 55 mm (thick line) are indicated. The map below represents the boundaries of the Ontígola municipality (continuous line), and the location of the 16 sites of the local sampling study. Squares A, B and C are the resting places for the three sheep-flocks; and the approximate home range of these flocks is shown in grey.

humid conditions. Here, local dung beetle assemblages comprise approximately half the species richness of nearby assemblages occurring in more humid Mediterranean pasturelands grazed by cows, where most species remain in the field 1 year after the disappearance of the livestock (Lobo *et al.*, 1998). Thus, as dry sheep dung is the main trophic resource, and the prevailing environmental conditions are semi-arid, we assume that changes in dung beetle community structure and species richness are likely to be easier to detect due to the faster response of these poor and easy to collect assemblages to the level of available resources.

The local sampling was made in an area of around 30 km², within the townships of Ontígola and Aranjuez (see Fig. 1), located between meadows at the lowest elevations (*c.* 500 m a.s.l.) and the moorlands (*c.* 700 m a.s.l.) of the Tajo Valley. This steppe-like locality (600–650 m a.s.l.) presents poor sedimentary gypsum soils of limited productivity, less than 500 mm of mean annual rainfall and mean annual temperatures around 15 °C. Mixed land use comprises medium-sized plots of non-intensive cereal cultivation, olive groves and vineyards, alternating with scattered trees or shrubs (*Quercus coccifera*, *Rhamnus lycioides*, *Stipa tenacissima* or *Gypsophila struthium*).

The locality is grazed only by sheep, with a small contribution from goats; the only other significant dung source is the abundant rabbit population. Sheep feed in almost permanently dry pasturelands in the intermittent watercourses, fallow areas (devoted to the cultivation of cereals in following years), stubble-fields (areas of harvested cereal), heaths, road borders and among olive groves. Three sheep flocks breed in the region, with relatively well-established grazing ranges, partially defined by

municipal boundaries (see Fig. 1). Flock A (around 480 head) grazes over a surface of approximately 1000 ha; flock B (410 head) does over 1400 ha; and flock C (300 head) over a 600-ha pastureland. Thus, around 1200 heads were present in the area during the study, with densities ranging from 0.3 to 0.5 sheep ha⁻¹, depending on the flock considered. However, sheep tend to concentrate on some localities, where they pass through or stay for longer, in some cases up to 250 days year⁻¹. When such densities occur, more than 50% of basic nutrients (nitrogen, phosphorous or potassium) in the soil would come from sheep dung, which is responsible for a notable boost to plant productivity (Breymer, 1974; Loiseau *et al.*, 1984; Ricou & Loiseau, 1984).

Data collection

Eighteen localities were sampled to obtain a picture of regional faunas. Sampling plots were spread over a 567-km² area (Fig. 1; Table 1) with a mean distance between them of 19.0 km (mean of the distances between all pairs of sites; ± 0.9 SE; maximum distance = 42.5 km, minimum distance = 1.6 km). In each locality 10 baited pitfall traps were used. Following the method recommended by Lobo *et al.* (1988) and Veiga *et al.* (1989), the pitfall traps were baited with 100 g of fresh sheep dung and the attracted beetles collected after 48 h. To capture the two main dung beetle phenologic peaks, five traps were placed 10 m apart in spring and another five in autumn. In Mediterranean conditions, dung beetles are usually more abundant and diverse in open biomes than in close ones, which also lack exclusive species (Lumaret & Kirk, 1987). Thus, sites without arboreal cover

Table 1 Spatial and environmental characteristics of the localities from the regional sampling. Spatial coordinates are in metres, referred to the UTM 30 N system, and altitude in metres a.s.l. Rainfall is given in mm, and temperature in Celsius degrees. Bovine and ovine herd density is given in livestock heads by km². The origin of the variables is explained in the text. Site numbers as in Fig. 1 (right map). N is the number of collected individuals whilst S is the number of species

| Locality | N | S | Longitude | Latitude | Altitude | Mean annual rainfall | Summer rainfall | Mean annual temperature | Density of bovine herds | Density of ovine herds |
|----------|-----|----|-----------|-----------|----------|----------------------|-----------------|-------------------------|-------------------------|------------------------|
| 1 | 55 | 8 | 480,886 | 4,434,266 | 532 | 453 | 54 | 14.3 | 23.0 | 8.4 |
| 2 | 57 | 7 | 487,940 | 4,433,972 | 634 | 457 | 54 | 14.3 | 19.4 | 8.8 |
| 3 | 528 | 9 | 483,970 | 4,437,125 | 565 | 451 | 54 | 14.3 | 16.6 | 7.7 |
| 4 | 147 | 13 | 481,298 | 4,429,256 | 594 | 462 | 54 | 14.2 | 19.5 | 8.8 |
| 5 | 475 | 13 | 436,482 | 4,416,740 | 507 | 412 | 58 | 12.6 | 22.5 | 9.6 |
| 6 | 58 | 8 | 430,633 | 4,415,801 | 548 | 413 | 57 | 12.8 | 25.2 | 9.7 |
| 7 | 139 | 8 | 438,068 | 4,411,307 | 574 | 412 | 58 | 12.6 | 23.1 | 11.9 |
| 8 | 109 | 11 | 435,064 | 4,414,976 | 522 | 412 | 58 | 12.6 | 21.8 | 9.6 |
| 9 | 80 | 14 | 438,000 | 4,423,850 | 520 | 414 | 56 | 12.9 | 21.9 | 9.7 |
| 10 | 95 | 11 | 438,732 | 4,426,519 | 475 | 419 | 53 | 13.4 | 21.6 | 9.6 |
| 11 | 288 | 8 | 432,575 | 4,427,995 | 591 | 419 | 51 | 13.6 | 31.9 | 9.9 |
| 12 | 60 | 6 | 440,620 | 4,438,045 | 584 | 429 | 48 | 14.2 | 39.7 | 9.6 |
| 13 | 30 | 8 | 446,185 | 4,432,970 | 476 | 425 | 50 | 14.0 | 32.2 | 9.7 |
| 14 | 19 | 7 | 448,017 | 4,435,812 | 525 | 425 | 50 | 14.0 | 31.4 | 10.3 |
| 15 | 21 | 6 | 463,963 | 4,437,743 | 620 | 434 | 51 | 14.0 | 21.5 | 10.1 |
| 16 | 19 | 4 | 468,050 | 4,432,405 | 539 | 445 | 52 | 14.1 | 18.9 | 9.5 |
| 17 | 283 | 10 | 459,880 | 4,432,554 | 491 | 426 | 50 | 14.0 | 22.9 | 10.3 |
| 18 | 157 | 12 | 470,961 | 4,441,185 | 675 | 452 | 54 | 14.1 | 13.9 | 9.7 |

were chosen for sampling (as well as in the local sampling; see description below). A complete discussion about the site allocation method used to select sampling plots, as well as about the selection of sampling dates, is given in Hortal (2004) and Hortal & Lobo (2005).

Sixteen sites were selected for the local sampling to describe small-scale variations in dung beetle spring fauna. The plots were spread through an approximate area of 36 km² (Fig. 1), with a mean distance between them of 3634 m (± 156 SE; maximum distance = 8039 m, minimum distance = 660 m). Geographical location and altitude of sampling sites was determined by Global Positioning System (see Table 2). Each site was sampled only one time in spring (7 and 10 June 1997), using five baited pitfall traps, as described for the regional inventory.

Such seasonally limited sampling allowed us to obtain a good representation of the studied local assemblages, and thus can be used to describe local variations due to resource availability. The spring inventory of Mediterranean local assemblages of dung beetles represents 70–80% of the complete annual inventory (Lobo *et al.*, 1997). More specifically, in Iberian semi-arid conditions the marked spring peak in abundance and species richness hosts around 74–81% of annual species (Sánchez-Piñero, 1994; Sánchez-Piñero & Ávila, 2004). Most of the remaining species (principally Aphodiinae) occur in autumn and winter, being the summer a period in which only a few individuals of several spring species can be collected. As the spring emergence of individuals of these assemblages in a given year would depend on the level of resources in the previous spring, not on the overall annual resource level, an annual sampling programme needs to concentrate on the effect of resource quantities during each spring peak

in dung beetle activity. In addition, the poor summer and autumn–winter assemblages should present little variation in species richness between localities, and the vegetal growth is higher and the shepherding more intense during spring. Therefore, the effect of resource quantities in dung beetle activity can be assessed using their responses to such spring peak. Thus, the sampling was limited to such season. Only five pitfall traps per locality were used, as such number has been proven enough to sample adequately the structure and composition of a dung beetle assemblage in Mediterranean conditions (Lobo *et al.*, 1998): although 15 traps collect 95% of the species present in a given site and five capture approximately 70% of them, these later species represent around 90% of total dung beetle abundance and total biomass. In our study, a unique trap collects an average 9% of all the species known for the region, and the group of five traps placed in each locality around 15% of that figure (see Results). With regard to the local study, the observed species richness was, respectively, 37% and 52% of the figures estimated and collected for the regional pool (see below).

To identify factors affecting diversity at a regional scale, 1-km² resolution GIS (Geographical Information System) data on the environmental conditions and grazing activity of each sampling plot from the regional sampling (see Table 1) was extracted from CM-SIG, a GIS database of Central Spain (Hortal, 2004; see also Hortal & Lobo, 2005). In this database, climate data (mean annual and summer precipitation and mean annual temperature) come from a mobile mean interpolation (IDRISI32 INTERPOL module; see Clark Labs, 2001), using 30-year mean data from 41 meteorological stations compiled in an agroclimatic atlas (MAPA, 1986). Substrate variables (not shown in the table) came from a regional atlas (bedrock lithology; ITGE, 1988) and

Table 2 Spatial and environmental characteristics of the sites from the local sampling. Spatial coordinates are in UTM metres and altitude in metres a.s.l. Cover is the area covered by vegetation (in m²) between 30 and 60 cm, and above 60 cm in height. First count is dry weight of sheep and rabbit dung (in g m⁻²) gathered along a 20-m² transect 2 months before carrying out the faunistic sampling in each of the sample sites. Second count is dry weight of dung (in mg day⁻¹ m⁻²) gathered in the same places 1 week before the faunistic sampling. Site numbers as in Fig. 1

| Site number | Longitude | Latitude | Cover 30–60 cm | Cover > 60 cm | Altitude | First count | | Second count | |
|-------------|-----------|-----------|-------------------|------------------|----------|-------------|-------|--------------|-------|
| | | | | | | Rabbit | Sheep | Rabbit | Sheep |
| 1 | 450,203 | 4,428,206 | 0.94 | 0.00 | 614 | 0.07 | 0.77 | 0.93 | 12.19 |
| 2 | 451,206 | 4,427,316 | 0.22 | 0.00 | 613 | 2.84 | 0.92 | 16.82 | 6.25 |
| 3 | 450,928 | 4,426,717 | 0.59 | 0.00 | 622 | 0.11 | 0.59 | 2.91 | 2.30 |
| 4 | 451,468 | 4,426,287 | 0.00 | 0.00 | 633 | 0.01 | 0.01 | 5.18 | 1.96 |
| 5 | 453,063 | 4,425,953 | 0.14 | 0.00 | 643 | 2.73 | 0.01 | 84.41 | 1.89 |
| 6 | 453,724 | 4,426,573 | 0.29 | 0.00 | 658 | 0.36 | 0.05 | 12.22 | 0.12 |
| 7 | 454,302 | 4,426,983 | 0.00 | 0.00 | 659 | 0.00 | 0.56 | 0.01 | 3.52 |
| 8 | 452,636 | 4,427,971 | 15.21 | 0.75 | 596 | 0.05 | 1.86 | 0.60 | 6.59 |
| 9 | 452,716 | 4,429,531 | 0.11 | 5.00 | 601 | 1.38 | 1.51 | 49.16 | 5.21 |
| 10 | 451,756 | 4,429,947 | 0.38 | 0.00 | 569 | 24.81 | 0.00 | 856.83 | 0.06 |
| 11 | 449,739 | 4,429,701 | 0.01 | 0.00 | 616 | 0.40 | 2.69 | 31.58 | 15.96 |
| 12 | 455,962 | 4,429,724 | 0.69 | 0.03 | 646 | 0.29 | 0.13 | 11.34 | 1.00 |
| 13 | 457,735 | 4,430,536 | 3.28 | 0.03 | 638 | 0.09 | 0.31 | 45.04 | 1.18 |
| 14 | 453,716 | 4,431,780 | 0.00 | 0.00 | 609 | 0.04 | 0.61 | 0.68 | 4.19 |
| 15 | 452,273 | 4,431,489 | 0.16 | 1.50 | 613 | 16.30 | 0.12 | 430.96 | 0.43 |
| 16 | 452,257 | 4,430,824 | 0.32 | 0.16 | 572 | 4.76 | 2.03 | 158.26 | 6.45 |

the FAO Soil Map of the World (FAO, 1988). Finally, data on the number of livestock per municipality were obtained from a socioeconomic atlas (Anonymous, 1998). Livestock density per municipality was calculated for three herd categories (cattle, sheep and goat and horse), being the so-obtained values associated to the centroid (or centroids) of each municipal polygon. Then, maps were generated using the same interpolation technique as for the climatic data.

In the case of local analysis, site data were obtained by direct field observations (see Table 2). To cover variations since the probable emergence of individuals, dung availability was measured in two different counts. Two months before carrying out the local sampling (at the beginning of the spring), all sheep and rabbit pellets were gathered along a 20-m² transect in each one of the sample sites (10 × 2 m; 'first count'). Afterwards, 1 week before carrying out the sampling, newly deposited pellets were gathered again ('second count'). In both occasions, dung dry weight was measured after 48 h at 75 °C. Together with measures of the amount of available trophic resources, vegetation cover between 30 and 60 cm in height, and above 60 cm, was measured for each one of the transects.

The amount of sheep dung in each one of the sample sites was used to build an interpolated map at a resolution of 100 × 100 m and the mean and maximum amount of sheep dung in a buffer of 2 km calculated for each sample site as a measure of the quantity of dung available in the surroundings of each collection point.

Analytical procedures

We plotted the species accumulation curves (500 randomizations) to ascertain if the number of captured species can be

considered a good approximation of actual species richness. Two widely used and efficient nonparametric estimators of species richness were also obtained: the abundance-based coverage estimator (ACE) and Chao2 (Colwell & Coddington, 1994). For these analyses, the EstimateS package (Colwell, 2000) was used, using the number of pitfall traps as sampling effort measure.

We used both species richness and abundance (in logarithm) within each local sampling site as dependent variables. For both regional and local data, multiple regression analysis was used to estimate the influence of environmental variables, standardizing the continuous predictors to avoid bias due to the differences in the units of measure. To find the best predictive model, a backward stepwise procedure was employed in which both the forward entry and the backward removal of variables are used (Legendre & Legendre, 1998). Curvilinear relationships between explanatory and predictor variables were examined, as well as the explanatory capacity of possible interactions among independent variables (Margules *et al.*, 1987).

If the residuals from the regression analysis are spatially structured, therefore being spatially autocorrelated, it is indicative that one or several important explanatory variables have been left out (Legendre & Legendre, 1998). The spatial distribution of these residuals can allow identifying which factors have not been considered (see Diniz-Filho *et al.*, 2003). Both explanatory variables and residuals of the obtained function were checked for spatial autocorrelation by calculating Moran's *I* spatial autocorrelation statistic with a Bonferroni-corrected significance level (Cliff & Ord, 1984; Sawada, 1999) to ascertain the spatial structure of these variables, as well as to provide an estimate of the reliability of the model obtained.

The comparative importance of each explanatory variable was established by variation partitioning (see MacNally, 2000). First, the percentage of variation explained by each one of the functions that can be developed with these explanatory variables (2^k , being k the number of predictors) is calculated. Then, the impact of each independent variable is estimated as the average effect of including such predictor in all the models built with the remaining variables (MacNally, 2000).

The Bray–Curtis similarity coefficient between localities or sites was computed using the log-transformed number of individuals of each species in each locality ($\log x + 1$). The triangular abundance similarity matrix so-obtained was subjected to a cluster analysis with the Ward method as linkage rule to describe the main groups of localities according to faunistic composition. Both Bray–Curtis coefficient and the Ward linkage rule were selected by its general well performance (Ludwig & Reynolds, 1988; Legendre & Legendre, 1998). The environmental differences among these faunistic groups of localities were analysed using nonparametric statistical test.

RESULTS

Sampling effectiveness

The sampled spring local dung beetle assemblages are not disproportionately poor by the lack of an adequate sampling effort. According to SCAMAD, an exhaustive database that compiles all the faunistic information available in the bibliography and natural history collections for Central Spain (Hortal, 2004), 59 dung beetle species have been recorded in the studied region. The spring inventory raised by our regional sampling comprises 42 of these species (71%). Interestingly, the unique annual exhaustive study on Iberian semi-arid dung beetle communities accomplished using a similar method (120 pitfall traps placed in three southeastern localities; Sánchez-Piñero & Ávila, 2004) collected 46 species. Moreover, our local sampling collected 22 species, a richness score quite similar to the figures found in that study (27, 25 and 31 in each locality, respectively). To the contrary, whilst mean individuals per site in these southeastern Iberian localities oscillated between 3 and 24 (Sánchez-Piñero & Ávila, 2004), in our regional study this figure was much higher (58.6 ± 136.7 SD). The abundance on the local study, however, was much smaller (5.6 ± 5.2 SD), due to the low scores of the sites with very low trophic resources. The spring mean species richness per trap (\pm SD) in the regional study was 5.2 ± 2.0 (3.4 ± 1.9 for all the year) and 2.6 ± 2.0 in the local one, while the mean richness per trap was around 3 in southeastern Iberian semi-arid region (Sánchez-Piñero & Ávila, 2004). On average, 9% of all the species known for the region were collected by a single trap in the regional survey, and a group of five traps placed per locality got around 15% of these species.

The regional inventory obtained from the 18 localities can be considered a representative sample of the spring inventory as observed species richness is 69% of predicted by ACE and 79% of predicted by Chao2 (SD = 14% in both cases). In the case of the local study, a nearly asymptotic richness value was attained as the

total number of species collected was 92% of that estimated by ACE and 96% of that estimated by Chao2. Moreover, when examining individual accumulation curves for each one of the 16 sites (not shown), all of them showed asymptotic trends, evidencing that the main assemblage composition was collected in each locality.

Regional analysis

None of the selected explanatory variables were significantly related to the logarithm of the number of individuals, and a backward stepwise regression analysis using the third-degree polynomial of latitude and longitude as predictors (trend surface analysis, TSA; see Legendre & Legendre, 1998) does not allow to explain the regional variation in abundance. Moran's I autocorrelation scores of the number of spring individuals (in logarithm) neither allowed to distinguish a spatial pattern (active lag distance = 30 km; lag class distance = 6000 m).

The only environmental variable significantly related to the number of spring species is the summer rainfall ($F_{1,16} = 5.72$; $P = 0.03$), which accounted for 26.3% of total variability in species richness. This relationship is linear and positive, so less species seem to occur in those localities with lower precipitation during the summer. Moran's I autocorrelation scores of the number of spring species do not show a clear spatial pattern and the TSA accomplished with the residuals of the former function as dependent variable does not also produce any significant relationship. Cluster analysis on species composition clearly discriminates three groups of localities (Fig. 2a; see locality characteristics at Table 1). The only environmental variable with significant differences between groups is altitude (Kruskall–Wallis ANOVA by ranks test = 6.34; $P = 0.04$), as the lower altitude localities located at the valleys seem to host compositionally different assemblages (localities 10, 13, 14, 16 and 17; mean altitude = 501 ± 21 m).

Local analysis

The amount of dung gathered in the first count is highly correlated to that of the second one (Spearman rank correlation, $r_s = 0.90$, $n = 16$; $P < 0.0001$ for rabbit dung, and $r_s = 0.89$, $n = 16$; $P < 0.0001$ for sheep dung). Thus, the sites with higher initial quantities of dung were those subsequently most visited by sheep or rabbits.

The occurrence of a gradient in the spatial variation of both total species richness and total abundance is shown by its correlograms (Fig. 3a,b), so nearby localities (up to 1 km or 1.5 km apart) share similar values of species richness or abundance, decreasing gradually and almost linearly the autocorrelation scores with the distance. However, the amount of sheep dung in both counts does not show any autocorrelated spatial structure, as the quantity present at any site is independent of the amount present in nearby localities (Fig. 3c).

None of the environmental explanatory variables are significantly related to the abundance of dung beetles, but a backward selection of the nine spatial terms of a third-degree

Figure 2 Dendrograms representing the similarity for (a) the 18 localities of the regional sampling and (b) the 16 sites of the local sampling. The Bray–Curtis similarity coefficient was used as measure of resemblance taking into account the log-transformed number of individuals of each species in each locality ($\log x + 1$), and the Ward method as linkage rule.

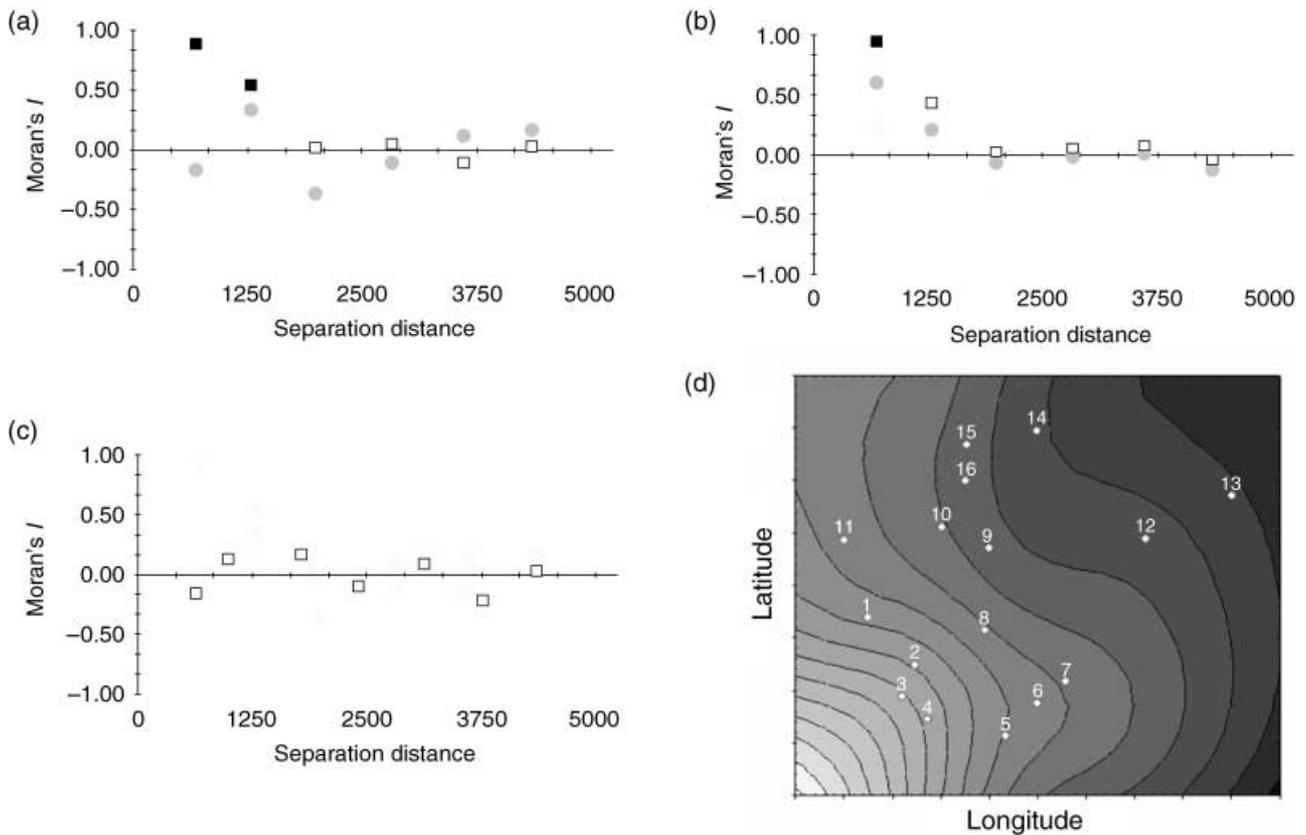
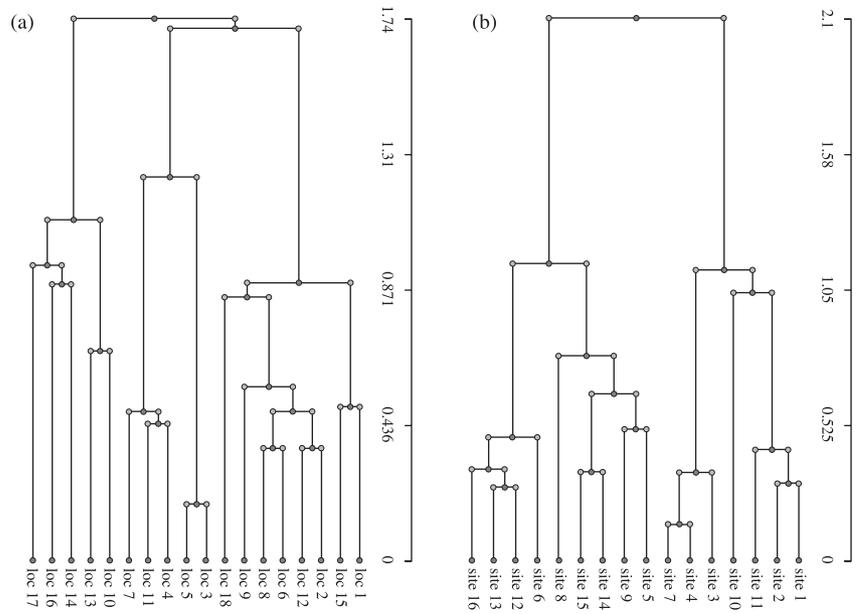


Figure 3 Isotropic correlograms representing the scores of Moran's *I* spatial autocorrelation statistic, with the separation distance between localities (in metres). Correlograms for total number of species per sampling site (a), abundance (b) and for quantity of sheep dung (c) in the second count (see Table 2). The correlograms were using a lag distance of 750 m and an active lag of 6000 m. Black squares present a Bonferroni-corrected significant Moran's *I* score (Sawada, 1999), while grey dots represent the autocorrelation scores of the obtained residuals after accomplishing a stepwise regression analysis with the environmental (species richness) or spatial (abundance) significant explanatory variables. (d) Contour plot of the spatial variation in the raw residuals of the function that relates the number of total species per sampling site in the local study to the quantity of sheep dung in the second count (Table 3). Positive vs. negative residuals scores are represented in a white to black gradient.

Table 3 Results of the regression analyses relating the total number of species per site (local sampling) with the environmental variables considered (Table 2)

| Explanatory variables | Coefficient | <i>t</i> | <i>P</i> | <i>R</i> ² |
|----------------------------|-------------|----------|----------|-----------------------|
| Cover 30–60 cm | –0.334 | –0.37 | 0.72 | 0.010 |
| Cover > 60 cm | –0.799 | –0.90 | 0.38 | 0.055 |
| Altitude | –0.091 | –0.10 | 0.92 | 0.001 |
| Rabbit dung (first count) | –0.590 | –0.66 | 0.52 | 0.030 |
| Rabbit dung (second count) | –0.729 | –0.82 | 0.43 | 0.045 |
| Sheep dung (first count) | 1.200 | 1.40 | 0.18 | 0.123 |
| Sheep dung (second count) | 1.776 | 2.28 | 0.04 | 0.270 |

polynomial of latitude and latitude selects the lineal term of latitude (44.08% of variance). The residuals of this spatial function significantly diminish the positive autocorrelation at low distances (Fig. 3a).

The amount of sheep dung observed at the second count is the only significant variable found, being positively related to species richness per sampling site (27% of explained variation; Table 3). The residuals of such function are normally distributed. However, the residuals presented an obvious spatial structure with negative scores (predicted scores greater than observed) in the northeastern zone and positive scores (predicted scores lower than observed) in the southwestern zone of the studied area (Fig. 3d). When the nine terms of a third-degree polynomial of latitude and longitude were submitted to a backward stepwise regression analysis with the residuals as dependent variable (TSA), the linear term of latitude, and a complex interaction term (latitude² × longitude), accounted for 60.13% of the variability in these residuals, showing they were spatially structured. The correlogram of these residuals also shows that spatial structure in species richness remains unexplained (Fig. 3b). Thus, an important variable acting in the surroundings of each site seems not included in the analysis.

The influence of nearby localities

The mean and maximum amount of sheep dung in a 2-km buffer was calculated for each one of the sites taking into account the scores of sheep dung at the second count. The mean quantity of dung in these nearby sites explain 60.36% of the variance in species richness ($b = 2.65$, $t = 4.62$, $P < 0.001$) and 27.41% of variance for the logarithm of abundance ($b = 0.20$, $t = 2.30$, $P < 0.04$). The maximum quantity of dung accounted for 65.74% of the variance in species richness ($b = 2.77$, $t = 5.18$, $P = 0.0001$) and 31.87% of variance for the number of individuals ($b = 0.22$, $t = 2.56$, $P < 0.02$). The residuals of these functions did not show any remaining spatial structure.

The effect of sheep flocks

Grouping the sampled sites by the area of influence of each flock (Fig. 1) reveals that area C has the greatest number of individuals, species and sheep density (0.5 head ha⁻¹). Adding the identity

of the flock that grazed at each site as a dummy independent variable, together with the quantity of sheep dung and the maximum quantity available within a radius of 2 km, leads to a model in which the only significant variable is the association with sheep flock C. This dummy variable explains 53.23% of the variance in the logarithm of abundance ($b = -0.29$, $t = 3.99$, $P = 0.001$) and 73.6% for species richness ($b = -3.02$, $t = 5.94$, $P < 0.001$). The residuals for these functions were not spatially autocorrelated at any lag distance.

Comparative importance of significant variables

We calculated all functions for the possible combinations of the three variables previously found to be more significant (sheep flock C, quantity of observed sheep dung at the second count and maximum quantity of sheep dung in localities separated by less than 2 km). For species richness, the mean percentage of explained variance was 35.02% for the dummy variable (sheep flock C), 28.85% for the maximum sheep dung in nearby sites and 6.97% for the sheep dung quantity in the site. In the case of abundance, the sheep flock C account for 33.11% of variance, 11.83% for the maximum sheep dung in nearby sites and 4.28% for the sheep dung quantity in the site.

Species composition

Cluster analysis identifies two main groups of sites in accordance to their faunistic composition (Fig. 2b). The first group (group I) includes sites 1, 2, 3, 4, 7, 10 and 11, and it is characterized by a significantly higher mean species richness (Mann–Whitney *U*-test, $Z = 2.91$, $P = 0.004$), a higher number of individuals ($Z = 2.75$, $P = 0.006$) and the dominance of the more ubiquitous species (*Onthophagus latigena*, *O. merdarius* and *Aphodius foetidus*). The second group (group II) contains the remaining sites characterized by lower species richness and abundance figures, and the dominance of *O. merdarius*, *O. ruficapillus* and *Euoniticellus fulvus* (see Table 4). Except one occasional species (*Aphodius tingens*, $n = 1$), all the species were collected in group I sites. Therefore, the species-poor group II sites can be considered a nested subsample of the species-rich group I assemblages (see Table 4). The explanatory variables that significantly differ between the two groups are the mean and maximum amount of sheep dung in the sites separated by less than 2 km ($Z = 2.27$, $P = 0.02$ and $Z = 2.43$, $P = 0.01$, respectively), being higher at group I sites.

Analysis by species

Only the five species with 20 or more individuals collected are analysed (Table 4). The only explanatory variable significantly related to the logarithm of the abundance of *O. merdarius* is the interaction between sheep and rabbit dung at the second count ($b = 0.747$, $t = 4.20$, $P < 0.001$), explaining 55.71% of the variance. Thus, it seems to indicate that the most favourable localities for this species are those with low densities of rabbit dung and moderate to low densities of sheep dung (Fig. 4). For

Table 4 Individuals of each species collected in the 16 local sampling sites (see Fig. 1). The most species-rich locality is in the leftmost column, while the most abundant species is in the top row, in order to show the nested distribution pattern of these assemblages; that is, a configuration pattern in which species poor sites are a subset of those species-rich sites. The nestedness temperature of this matrix is 19.07 °C (a measure of the extent of order in the matrix) while the mean temperature of 500 randomized matrices is 52.23 ± 6.67 °C, being 3.5×10^{-7} the Monte Carlo-derived probability that this matrix was randomly generated (see Atmar & Patterson, 1993)

| Group | I | I | I | I | I | II | I | II | I | II | II | II | II | II | II | Total | |
|--|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-------|-----|
| Site number | 2 | 11 | 3 | 1 | 4 | 6 | 7 | 8 | 10 | 16 | 5 | 9 | 15 | 12 | 14 | 13 | |
| <i>Onthophagus (Palaeonthophagus) merdarius</i> | 11 | 6 | 24 | 8 | 34 | 10 | 33 | 4 | | 11 | 4 | 4 | 3 | 12 | 4 | 8 | 176 |
| <i>Onthophagus (Palaeonthophagus) latigena</i> | 8 | 13 | 20 | 10 | 21 | 2 | 26 | 1 | 3 | | 4 | | | | | | 108 |
| <i>Aphodius (Aphodius) foetidus</i> | 7 | 6 | 11 | 5 | | | 1 | | 1 | 1 | | | 1 | | 1 | | 34 |
| <i>Euoniticellus fulvus</i> | 5 | 8 | 1 | 2 | | 3 | | 5 | | | | | 3 | 1 | | | 28 |
| <i>Onthophagus (Furconthophagus) furcatus</i> | 1 | 5 | 6 | 2 | 1 | | 2 | | | | 2 | 1 | | | | | 20 |
| <i>Onthophagus (Palaeonthophagus) ruficapillus</i> | | 2 | | | | 1 | | 8 | | 2 | | 1 | | | | | 14 |
| <i>Aphodius (Bodilus) ictericus</i> | 3 | 4 | 1 | 2 | 1 | | | | | | | | | | | | 11 |
| <i>Aphodius (Calamosternus) granarius</i> | | | 3 | | | 3 | 2 | | | | | | | 1 | 1 | | 10 |
| <i>Onthophagus (Palaeonthophagus) vacca</i> | 1 | 3 | 1 | | 1 | | | 3 | | | | | | | | | 9 |
| <i>Onthophagus (Relictonthophagus) emarginatus</i> | | 3 | 1 | | 1 | | | | 2 | | 1 | | | | | | 8 |
| <i>Euoniticellus pallipes</i> | | | 3 | 1 | | | | 3 | | | | | | | | | 7 |
| <i>Aphodius (Otophorus) haemorrhoidalis</i> | | | | 1 | 1 | | | | | 2 | | | | | | | 4 |
| <i>Onthophagus (Onthophagus) taurus</i> | | | | | 1 | | | | 1 | 2 | | | | | | | 4 |
| <i>Aphodius (Chilothorax) distinctus</i> | 1 | | | | | 1 | 1 | | | | | | | | | | 3 |
| <i>Aphodius (Chilothorax) lineolatus</i> | 1 | | | | | | | | | 1 | | | 1 | | | | 3 |
| <i>Onthophagus (Palaeonthophagus) opacicollis</i> | 1 | 2 | | | | | | | | | | | | | | | 3 |
| <i>Aphodius (Colobopterus) erraticus</i> | | | | 2 | | | | | | | | | | | | | 2 |
| <i>Gymnopleurus sturmi</i> | 1 | | | | 1 | | | | | | | | | | | | 2 |
| <i>Onitis belial</i> | 1 | | | | | | 1 | | | | | | | | | | 2 |
| <i>Aphodius (Acanthobodilus) immundus</i> | | | | 1 | | | | | | | | | | | | | 1 |
| <i>Aphodius (Aphodius) fimetarius</i> | 1 | | | | | | | | | | | | | | | | 1 |
| <i>Aphodius (Melinopterus) tingens</i> | | | | | | | | | | | | | | 1 | | | 1 |
| Total individuals | 42 | 58 | 69 | 31 | 61 | 21 | 65 | 24 | 9 | 17 | 11 | 9 | 6 | 14 | 6 | 8 | 451 |
| Total species | 13 | 12 | 11 | 8 | 8 | 7 | 6 | 6 | 5 | 5 | 4 | 4 | 4 | 3 | 3 | 1 | |
| Mean species richness per trap | 5.6 | 6.4 | 5.2 | 3.0 | 3.2 | 2.6 | 3.0 | 2.8 | 1.6 | 1.8 | 1.8 | 1.4 | 1.0 | 1.4 | 1.0 | 0.6 | |

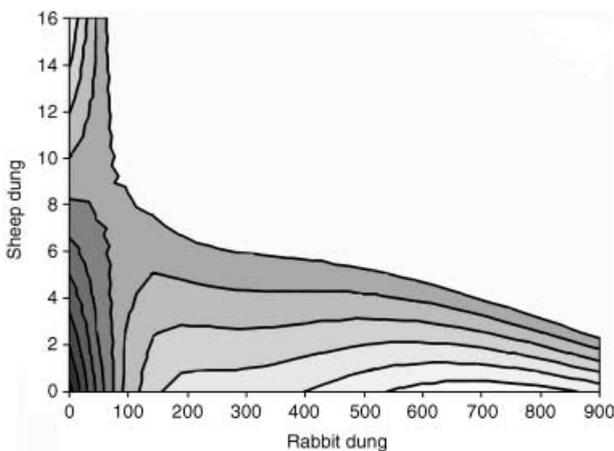


Figure 4 Contour plot of the total number of individuals of *Onthophagus merdarius* in the space delimited by sheep and rabbit dung quantity scores present in the local study area. Grey intensities are directly proportional to number of individuals. The region outside the lines represents combinations of variables not present in the study area.

both *O. latigena* and *O. furcatus*, the only significant variable is the association with sheep flock C ($b = 0.421, t = 3.93, P = 0.001$; and $b = 0.491, t = 3.61, P = 0.003$), which explains, respectively, 52.41% and 48.23% in the variability of abundance among sites. In the cases of *E. fulvus* and *A. foetidus*, sheep dung at the second count was significantly and positively related to abundance ($b = 0.491, t = 2.90, P = 0.01$; and $b = 0.459, t = 2.34, P = 0.03$) accounting for 37.54% and 28.15% of variance, respectively. For *A. foetidus*, the flock C dummy variable explains an even higher percentage of variance (55.34%).

DISCUSSION

Both regional and local inventories seem to give a relatively good picture of the dung beetle fauna present in such semi-arid assemblages, assuring the reliability of the obtained results. From a regional-scale point of view, the main differences in dung beetle species richness and taxonomic composition across a relatively uniform semi-arid region of around 600 km² seem to be related to environmental changes. Although presenting slight differences among localities, total summer precipitation and altitude clearly discriminate the most arid localities from those located in the

valleys, where more permanent pasturelands are located. However, the variation in dung beetle abundance does not seem to be related to none of the used variables and the variation in the number of individuals seems to be more difficult to predict at this resolution. Interestingly, the effect of resource quantity cannot be detected at this resolution, appearing as a highly outstanding factor when the variation among environmentally homogeneous and spatially closer sites was analysed.

The efficiency of the variables related to the quantity of trophic resources to understand the local spatial variation in species richness, taxonomic composition and even abundance helps to understand the scale at which the influence of the amount of dung on the diversity of dung beetle assemblages can be perceived. Thus, the differences in the availability and quantity of trophic resources among nearby sites separated around 3 km could be affecting the population dynamics and dispersion of dung beetles within a locality (see Maurer, 2002). Although the colinearity among explanatory variables hinders to infer causes from correlations, variation partitioning analysis results suggest that the identity of the flock seems to be the most important variable to explain the local variation in dung beetle richness and abundance. However, their effect does not exclude the relevance of the other important variables: the quantity of dung in each site and the quantity in their surroundings. Local species richness of a given group in a given site has been related to ecosystem productivity and resource availability (see, e.g. Tilman *et al.*, 1997). In our studied locality, the amount of trophic resources in each site is not able to explain by itself the spatial variations in dung beetle abundance, species richness or taxonomic composition, and the amount of available resources in the surroundings (1 km or 2 km) must be considered. Both species richness and the number of individuals are variables that show a spatial autocorrelated pattern. On the contrary, the amount of sheep dung in one locality is not spatially autocorrelated, probably because flocks follow predetermined routes or directions. This difference in the spatial structure suggests that variations in biological parameters (species richness or abundance) are not completely linked to local variations in the quantity of dung. Such spatial autocorrelated structure also indicates that dung beetle assemblages are not spatially independent at the analysed resolution, as the amount of dung in the surroundings is more important for locally collected species than the dung effectively found in the site.

The faunistic homogeneity among assemblages should increase when distance between 'source sites' diminishes, even more if movements between local populations are frequent. Accordingly, increases in distance and/or decreases in trophic resources should result in incremental faunistic differences, decreases in intersite movements and the uncoupling of local population dynamics across the region (Hanski & Gilpin, 1997; Hubbell, 2001). In the studied locality, the average amount of sheep dung per site was $4.3 \text{ mg day}^{-1} \text{ m}^{-2}$, and the mean distance between sites with dung quantities higher than this mean score was 3.2 km. Under these circumstances, sites with larger populations and greater species numbers would not be able to exercise enough influence as to bring about a complete local faunistic homogenization. Thus, an appropriate separation of the sites

with great amounts of trophic resources can cause the observed dissimilarity between local assemblages.

There are three possible, although not incompatible, explanations for the capture of specimens in sites with small amounts of sheep dung: (1) these individuals are able to maintain viable populations in spite of scarce trophic resources; (2) they could consume other dung types, such as rabbit pellets; and (3) they could have arrived from nearby sites with sufficient trophic resources. The nested structure of site assemblages and the detection of two compositional groups of sites that differ in their richness, abundance and quantity of trophic resources, suggest that when trophic resources diminish, generally only the most abundant species from the 'source sites' seem to be able to colonize scarce trophic-resource sites. Colonization ability on a local scale is assumed to be density-dependent (Hanski *et al.*, 1993), but species-specific adaptations related to environmental tolerance or dispersal ability also could explain the regional presence of some dung beetle species (Roslin, 2000; Roslin & Koivunen, 2001). Some Mediterranean dung beetle species, such as *O. latigena* and *O. emarginatus*, are frequently collected in rabbit pellets (Sánchez-Piñero & Ávila, 1991; Galante & Cartagena, 1999) as, in dung beetles, endemism to Iberia is related to the density of rabbit populations (Verdú & Galante, 2002). Thus, rabbit dung and small amounts of human or dog excrement could contribute to the population maintenance of some species when traditional sheep grazing disappears. However, in this study, the most abundant species (*O. merdarius*) is the only one seems not influenced by the amount of sheep dung or by the presence/absence of the flock with the greatest dung renewal.

The ability to maintain assemblages in resource-poor sites with available trophic resources of wild herbivores such as rabbits may be elucidated by studying the assemblages that inhabit similar localities not grazed by sheep flocks. If the individuals collected in scarce trophic-resource sites coming from the populations inhabiting nearby sites with greater amounts of dung, then these species-poor assemblages would be nested subsets, an impoverished sample of those in species-rich sites (Atmar & Patterson, 1993). In this situation, local populations in unfavourable sites are maintained by colonization, and spatial autocorrelation would be the general rule, as seems to be the case of this study and others (Roslin & Koivunen, 2001). In an extreme situation, patchy livestock distribution would completely isolate local dung beetle assemblages separated by ungrazed areas.

It is clear from the results presented here that grazing intensity (and its associated increase in the amount of trophic resources) is a key factor in determining local variation in the diversity and composition of dung beetle assemblages, both because of its local influence and its effect on neighbouring assemblages. The radius of influence of increased grazing does not seem to exceed 1 km or 2 km; a quite similar pattern was estimated by Roslin (2000) in capture-recapture results, where movements between pastures were infrequent (see also Hanski, 1980). Interestingly, the supposed high dispersal capacity of a group adapted to the active search of an ephemeral resource is not supported by empirical evidences. Although between-species traits affecting potential colonization ability probably can show great variation, the influence

of passive and human-induced livestock movements should be studied in order to understand the implied mechanisms in the high distribution range expansions of some introduced species (between 50 and 220 km year⁻¹; Montes de Oca & Halffter, 1997).

While dung amount (resource availability) seems to determine local variation in dung beetle diversity, other related factors, such as grazing-pressure history and management regime also seem to be critical. It is known that when the grazing regime changes from sheep to cattle, both composition and abundance of dung beetles adjust to the new conditions (Lumaret *et al.*, 1992). Also, in localities where cattle grazing are continuous in time and great in numbers, the diversity and abundance of dung beetles is remarkably higher than in recently grazed localities (Lobo *et al.*, 1998). This allows habitats historically poor in dung beetle species, such as Mediterranean forests (see Kadiri *et al.*, 1997), to become as rich as nearby grazed pasturelands. In the present case, the influence of the management regime could contribute decisively to the importance of the sheep-flock dummy variable. As more sheep graze in a smaller area, dung is quickly renovated, favouring larger populations both in each site and in the surroundings. Hence, number of livestock, grazing history, distance between grazed localities and rate of dung renovation are key factors for the local variation in dung beetle diversity. As environmental differences among localities seem to be more influential than differences in the quantity of resources and their renovation rate at a regional scale, such a resource-dependent pattern would only be detected when this local scale source of variation is not obscured by small-scale environmental variability.

The abandonment of traditional pastoral systems, the halting of grazing in many localities, the irregular and spatially aggregated distribution of grazing and the growth of the livestock numbers fed with imported products are probably impoverishing the diversity of dung beetle assemblages (Lobo, 2001; Pitkänen & Roslin, 2001; Roslin & Koivunen, 2001). However, dung beetle activity in Mediterranean conditions is meant to be of crucial importance both in nutrient cycles and also probably in the dispersal of seeds contained in mammal droppings (see Andresen, 2003 for tropical biomes). In these circumstances, it is necessary to determine: (1) if the complete abandonment of livestock grazing activity in a locality leads to the disappearance of the associated dung beetle assemblages; (2) the capacity of local recolonization with livestock reintroduction; and (3) the role played by grazing intensity and by the distance among grazed sites in this recolonization process. Then the extent of the current alteration process of dung beetle assemblages, as well as the possibility of reversing it, could also be determined.

ACKNOWLEDGEMENTS

We are especially thankful to James Cerne, who helped us with the English review. This paper was supported by the projects REN2001-1136/GLO (Spanish D.G.I) and 07M/0080/2002 (Comunidad de Madrid). J.H. was supported by a PhD Museo Nacional de Ciencias Naturales/C.S.I.C./Comunidad de Madrid grant, and F.C.-S. by a PhD grant from the Ministerio de Educación y Cultura y Deporte.

REFERENCES

- Andresen, E. (2003) Effect of forest fragmentation on dung beetle communities and functional consequences for plant regeneration. *Ecography*, **26**, 87–97.
- Andrzejewska, L. & Gyllenberg, G. (1980) Small herbivore subsystem. *Grasslands, systems analysis and man* (ed. by A.I. Breymer and G.M. van Dyne), pp. 201–267. Cambridge University Press, New York.
- Anonymous (1998) *InfoMuni 98 Información Municipal de la Comunidad de Madrid*. CD-ROM Instituto de Estadística, Consejería de Hacienda, Comunidad de Madrid, Madrid.
- Atmar, W. & Patterson, B.D. (1993) The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia*, **96**, 373–382.
- Barbero, E., Palestrini, C. & Rolando, A. (1999) Dung beetle conservation: effects of habitat and resource selection (Coleoptera: Scarabaeidae). *Journal of Insect Conservation*, **3**, 75–84.
- Beaufoy, G., Baldock, D. & Clark, J., eds. (1995) *The nature of farming: low intensity farming systems in nine European countries*. WWF, IEEP & Joint Nature Conservation Committee, London.
- Bernáldez, F.G. (1991) Ecological consequences of the abandonment of traditional land use system in Central Spain. *Options Mediterraneennes*, **15**, 25–30.
- Bernáldez, F.G. (1992) Características esenciales de la naturaleza mediterránea. *Paisaje Mediterráneo*, pp. 42–45. Electa, Milano.
- Biström, O., Silfverberg, H. & Rutanen, I. (1991) Abundance and distribution of coprophilous Histerini (Histeridae) and *Onthophagus* and *Aphodius* (Scarabaeidae) in Finland (Coleoptera). *Entomologia Fennica*, **2**, 53–66.
- Bornemissza, G.F. (1976) The Australian dung beetles project 1965–75. *Australian Meat Research Commission Review*, **30**, 1–30.
- Breymer, A. (1974) Analyses of a sheep pasture ecosystem in the Pieniny mountains (the Carpathians). XI. The role of coprophagous beetles (Coleoptera, Scarabaeidae) in the utilization of sheep dung. *Ekologia Polska*, **22**, 617–634.
- Cambefort, Y. (1991) Biogeography and evolution. *Dung beetle ecology* (ed. by I. Hanski and Y. Cambefort), pp. 51–68. Princeton University Press, Princeton, NJ.
- Clark Labs (2001) *IDRISI 32 RELEASE 2*. GIS software package. Clark Laboratories, Worcester, MA.
- Cliff, A.D. & Ord, J.K. (1984) *Spatial processes. Models and applications*. Pion, London.
- Colwell, R.K. (2000) *EstimateS* v. 6.0b1. Computer program and manual available at <http://viceroy.eeb.uconn.edu/EstimateS>.
- Colwell, R.K. & Coddington, J.A. (1994) Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London. Series Biological Sciences*, **345**, 101–118.
- Diniz-Filho, J.A.F., Bini, L.M. & Hawkins, B.A. (2003) Spatial autocorrelation and red herrings in geographical ecology. *Global Ecology and Biogeography*, **12**, 53–64.
- FAO (1988) *Soil map of the world*. FAO/UNESCO, Rome.
- Fincher, G.T. (1981) The potential value of dung beetles in pasture ecosystems. *Journal of the Georgia Entomological Society*, **16**, 316–333.

- Finn, J.A. & Giller, P.S. (2002) Experimental investigations of colonisation by north temperate dung beetles of different types of domestic herbivore dung. *Applied Soil Ecology*, **20**, 1–13.
- Fry, R. & Lonsdale, D. (1991) Grassland habitats. *Habitat conservation for insects — a neglected green issue* (ed. by R. Fry and D. Lonsdale), pp. 93–115. The Amateur Entomologists' Society, Middlesex.
- Galante, E. & Cartagena, M.C. (1999) Comparison of Mediterranean dung beetles (Coleoptera: Scarabaeoidea) in cattle and rabbit dung. *Environmental Entomology*, **28**, 420–424.
- Gittings, T. & Giller, P.S. (1998) Resource quality and the colonisation and succession of coprophagous dung beetles. *Ecography*, **21**, 581–592.
- Gittings, T., Giller, P.S. & Stakelum, G. (1994) Dung decomposition in contrasting temperate pastures in relation to dung beetle and earthworm activity. *Pedobiologia*, **38**, 455–474.
- Gómez Sal, A., Rodríguez, M.A. & de Miguel, J.M. (1992) Matter transfer and land use by cattle in a dehesa ecosystem of Central Spain. *Vegetatio*, **99–100**, 345–354.
- Hanski, I. (1980) Spatial patterns and movements in coprophagous beetles. *Oikos*, **34**, 293–310.
- Hanski, I. & Gilpin, M.E., eds. (1997) *Metapopulation biology: ecology, genetics and evolution*. Academic Press, London.
- Hanski, I., Kouki, J. & Halkka, A. (1993) Three explanations of the positive relationship between distribution and abundance of species. *Species diversity in ecological communities* (ed. by R.E. Ricklefs and D. Schluter), pp. 108–116. University of Chicago Press, Chicago, IL.
- Holter, P. (1975) Energy budget of a natural population of *Aphodius rufipes* larvae (Scarabaeidae). *Oikos*, **26**, 177–186.
- Holter, P. (1982) Resource utilization and local coexistence in a guild of scarabaeid dung beetles (*Aphodius* spp.). *Oikos*, **39**, 213–227.
- Hortal, J. (2004) *Selección y Diseño de Áreas Prioritarias de Conservación de la Biodiversidad mediante Sinecología. Inventario y modelización predictiva de la distribución de los escarabeidos coprófagos (Coleoptera, Scarabaeoidea) de Madrid*. PhD Thesis, Universidad Autónoma de Madrid, Madrid.
- Hortal, J. & Lobo, J.M. (2005) An ED-based protocol for the optimal sampling of biodiversity. *Biodiversity and Conservation*, in press.
- Hortal-Muñoz, J., Martín-Piera F. & Lobo J.M. (2000) Dung beetle geographic diversity variation along a western Iberian latitudinal transect (Col., Scarabaeidae). *Annals of the Entomological Society of America*, **93**, 235–243.
- Hubbell, S.P. (2001) *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, NJ.
- Hutton, S.A. & Giller, P.S. (2003) The effects of the intensification of agriculture on northern temperate dung beetle communities. *Journal of Applied Ecology*, **40**, 994–1007.
- Hutton, S.A. & Giller, P.S. (2004) Intra- and interspecific aggregation of north temperate dung beetles on standardised and natural dung pads: the influence of spatial scale. *Ecological Entomology*, **29**, 594–605.
- ITGE (1988) *Atlas Geocientífico y del Medio Natural de la Comunidad de Madrid*. Instituto Tecnológico GeoMinero de España, Madrid.
- Kadiri, N., Lobo, J.M. & Lumaret, J.P. (1997) Conséquences de l'interaction entre préférences pour l'habitat et quantité de ressources trophiques sur les communautés d'insectes coprophages (Coleoptera, Scarabaeidae). *Acta Oecologica*, **17**, 107–119.
- Legendre, P. & Legendre, L. (1998) *Numerical ecology. 2nd English edn*. Elsevier, Amsterdam.
- Lobo, J.M. (2001) Decline of roller dung beetle (Scarabaeinae) populations in the Iberian Peninsula during the 20th century. *Biological Conservation*, **97**, 43–50.
- Lobo, J.M., Martín-Piera, F. & Veiga, C.M. (1988) Las trampas pitfall con cebo, sus posibilidades en el estudio coprófagos de Scarabaeoidea (Col.). I. Características determinantes de su capacidad de captura. *Revue d'Écologie et de Biologie Du Sology*, **25**, 77–100.
- Lobo, J.M., Sanmartín, I. & Martín-Piera, F. (1997) Diversity and spatial turnover of dung beetle (Coleoptera: Scarabaeoidea) communities in a protected area of south Europe (Doñana National Park, Huelva, Spain). *Elytron*, **11**, 71–88.
- Lobo, J.M., Lumaret, J.P. & Jay-Robert, P. (1998) Sampling dung-beetles in the French Mediterranean area: effects of abiotic factors and farm practices. *Pedobiologie*, **42**, 252–266.
- Loiseau, P., Jauneau, A. & Ricou, G. (1984) Études sur le recyclage dans l'écosystème prairial. I. Influence de la conduite du pâturage sur l'activité biologique des pelouses montagnardes. *Acta Oecologica*, **5**, 23–41.
- Ludwig, J.A. & Reynolds, J.F. (1988) *Statistical ecology*. John Wiley & Sons, New York.
- Lumaret, J.P. (1990) *Atlas de coleoptères Scarabeides Laparosciti de France*. Museum National d'Histoire Naturelle, Secretariat de la Faune et de la Flore, Paris.
- Lumaret, J.P. & Kirk, A. (1987) Ecology of dung beetles in the French Mediterranean region (Coleoptera: Scarabaeidae). *Acta Zoologica Mexicana*, **24**, 1–60.
- Lumaret, J.P., Kadiri, N. & Bertrand, M. (1992) Changes in resources: consequences from the dynamics of dung beetle communities. *Journal of Applied Ecology*, **29**, 349–356.
- MacNally, R. (2000) Regression and model-building in conservation biology, biogeography and ecology: the distinction between — and reconciliation of — 'predictive' and 'explanatory' models. *Biodiversity and Conservation*, **9**, 655–671.
- MAPA (1986) *Atlas agroclimático nacional de España*. 2nd edn. Ministerio de Agricultura Pesca y Alimentación, Dirección General de la Producción Agraria, Subdirección General de la Producción Vegetal, Madrid.
- Margules, C.R., Nicholls, A.O. & Austin, M.P. (1987) Diversity of *Eucalyptus* species predicted by a multi-variable environmental gradient. *Oecologia*, **71**, 229–232.
- Martín-Piera, F. & Lobo, J.M. (1995) Diversity and ecological role of dung beetles in Iberian grassland biomes. *Farming on the edge: the nature of traditional farmland in Europe* (ed. by D.I. McCracken, E.M. Bignal and S.E. Wenlock), pp. 147–153. Joint Nature Conservation Committee, Peterborough.
- Martín-Piera, F. & Lobo, J.M. (1996) A comparative discussion of trophic preferences in dung beetle communities. *Miscel Lànica Zoològica*, **19**, 13–31.

- Maurer, B. (2002) Predicting distribution and abundance: thinking within and between scales. *Predicting species occurrences. Issues of accuracy and scale* (ed. by J.M. Scott, P.J. Heglund, M.L. Morrison, J.B. Haufler, M.G. Raphael, W.A. Wall and F.B. Samson), pp. 125–132. Island Press, Washington, D.C.
- Montes de Oca, E. & Halffter, G. (1997) Invasion of Mexico by two dung beetles previously introduced into the United States. *Studies on Neotropical Fauna and Environment*, **33**, 37–45.
- Pitkänen, M. & Roslin, T. (2001) Dung beetles. *Biodiversity of agricultural landscapes in Finland* (ed. by M. Pitkänen and J. Tiainen), pp. 81–89. BirdLife Finland, Helsinki.
- Ricou, G. & Loiseau, P. (1984) Études sur le recyclage dans l'écosystème prairial. II. Coprophages et recyclage dans les pelouses montagnardes. *Acta Oecologica*, **5**, 319–334.
- Roslin, T. (2000) Dung beetle movement at two spatial scales. *Oikos*, **91**, 323–335.
- Roslin, T. & Koivunen, A. (2001) Distribution and abundance of dung beetles in fragmented landscapes. *Oecologia*, **127**, 69–77.
- Ruiz, J.P. & Ruiz Pérez, M. (1984) Environmental perception, livestock management and rural crisis in Sierra de Guadarrama (Madrid, Spain). *Acta Biologica Montana*, **4**, 455–466.
- Sánchez-Piñero, F. (1994) *Ecología de las comunidades de coleópteros coprófagos en zonas áridas de la Depresión de Guadix-Baza (Sureste de la Península Ibérica)*. PhD Thesis, Universidad de Granada, Granada.
- Sánchez-Piñero, F. & Ávila, J.M. (1991) Análisis comparativo de los Scarabaeoidea (Coleoptera) coprófagos de las deyecciones de conejo (*Oryctolagus cuniculus* (L.)) y de otros mamíferos. Estudio preliminar. *Eos*, **67**, 23–24.
- Sánchez-Piñero, F. & Ávila, J.M. (2004) Dung-insect composition in arid zones of south-eastern Spain. *Journal of Arid Environments*, **56**, 303–327.
- Sawada, M. (1999) ROOKCASE: An Excel 97/2000 visual basic (VB) add-in for exploring global and local spatial autocorrelation. *Bulletin of the Ecological Society of America*, **80**, 231–234.
- Suarez Cardona, F., Sainz Ollero, H., Santos Martínez, T. & González Bernáldez, F. (1992) *Las estepas ibéricas*. MOPT, Madrid.
- Tilman, D., Naeem, S., Knops, J., Reich, P., Siemann, E., Wedin, D., Ritchie, M. & Lawton, J. (1997) Biodiversity and ecosystem properties. *Science*, **278**, 1865c.
- Veiga, C.M., Martín-Piera, F. & Lobo, J.M. (1989) Las trampas pitfall con cebo, sus posibilidades en el estudio coprófagos de Scarabaeoidea (Col.). II. Análisis de efectividad. *Revue d'Écologie et de Biologie du Sology*, **26**, 91–109.
- Verdú, J.R. & Galante, E. (2002) Climatic stress, food availability and human activity as determinants of endemism patterns in the Mediterranean region: the case of dung beetles (Coleoptera, Scarabaeoidea) in the Iberian Peninsula. *Diversity and Distributions*, **8**, 259–274.
- Verdú, J.R., Crespo, M.B. & Galante, E. (2000) Conservation of a nature reserve in Mediterranean ecosystems: the effects of protection from grazing on biodiversity. *Biodiversity and Conservation*, **9**, 1707–1721.

