Effect of Elevation and Type of Habitat on the Abundance and Diversity of Scarabaeoid Dung Beetle (Scarabaeoidea) Assemblages in a Mediterranean Area from Southern Iberian Peninsula

Eduardo Romero-Alcaraz* and José M. Ávila

Departamento de Biología Animal y Ecología, Universidad de Granada, Campus de Fuentenueva, E-18071, Granada, Spain
Fax: 34-958-243238.   E-mail: eduardo@goliat.ugr.es

Eduardo Romero-Alcaraz and José M. Ávila (2000) Effect of elevation of type of habitat on the abundance and diversity of Scarabaeoid dung beetle (Scarabaeoidea) assemblages in a Mediterranean area from Southern Iberian Peninsula. *Zoological Studies* **39**(4): 351-359. Elevation and habitat type are often important factors influencing insect communities. We used dung-baited pitfall traps to test the effect of both elevation and habitat type on scarabaeoid dung beetle communities in Sierra de Baza (southeastern Iberian Peninsula). Habitat selection of species and variations of diversity in the assemblages according to habitat type and elevation were quantified. Both abundance and diversity were positively correlated with elevation, and habitat type was also relevant in structuring the assemblage. Similarities among assemblages in different biotopes were generally low, especially between closed habitats and open habitats, the latter showing higher abundance and diversity. Most species were less abundant in closed habitats, but some generalist species showed no habitat selection. We conclude that, although open habitats appear more adequate for dung beetles, the existence of different patterns within the assemblage probably reflects the importance of maintaining a high landscape heterogeneity in order to preserve dung beetle biodiversity.

Key words: Habitat selection, Dung beetle biodiversity, Elevational effect, Scarabaeidae, Aphodiidae.

Dung beetle communities comprise species with special ecological requirements due to the ephemeral and patchy nature of dung (Mohr 1943, Hanski 1987). Dung decomposes progressively and changes with time, with moisture loss being one of the most important factors determining the composition of coprophilous communities (Lobo 1991), although the way in which beetles and other organisms consume the resource is also relevant (Anderson and Coe 1974, Lobo 1991, Hirschberger and Bauer 1994). The ways in which dung decomposes and is used by coprophagous insects generate particular successional patterns that have been extensively studied (Mohr 1943, Koskela and Hanski 1977, Desiére 1987). Dung decomposition patterns and rates, and its potential colonization by beetles depend to a large extent on climatic and habitat characteristics like temperature, rain, soil humidity, or soil type (Landin 1967, Koskela 1972, Ávila and Fernández-Sigler 1988, Sánchez-Piñero and Ávila 1991, Sowig and Wassmer 1994). Elevation and habitat type, often acting together (Menéndez and Gutiérrez 1996), clearly influence the microclimate surrounding dung pats (Koskela and Hanski 1977), so habitat selection by dung beetles often occurs. As a consequence of this, beetle communities tend to differ among habitat types due to differential selection by species. In addition, because competition in patchy and ephemeral habitats is often strong (Hanski 1987), differential habitat selection may lead to effective spatial separation of species (Giller and Doube 1994), thus coexistence of species in an area may be favored by the existence of different biotopes.

In this paper we analyze the effects of elevation and habitat type on the scarabaeoid dung beetle assemblage in the Sierra de Baza Natural Park, southeastern Iberian Peninsula. We hypothesize that

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*To whom correspondence and reprint requests should be addressed.

habitat features promote selection by scarabaeoid dung beetle species, and thus are responsible for differences in the composition, abundance, and diversity of assemblages.

METHODS

Study area

The study area is located in the Sierra de Baza, southeastern Iberian Peninsula (37°20'N, 2°48'W). Sierra de Baza is a mid-elevation mountain system ranging from 900 to 2271 m. The climate is strongly Mediterranean, with mean temperatures varying from 3 °C in the coldest month to 23 °C in the warmest month (Medina and Chirosa 1992). Annual rainfall is scarce, at between 313 to 540 mm (Gómez-Mercado and Valle-Tendero 1988, Medina and Chirosa 1992). Sierra de Baza has been largely exploited by man through mining, agriculture, and livestock (Muñoz 1992). Therefore, the original vegetation is modified, mainly at the lower elevations; nevertheless, extensive areas at high elevations remain almost undisturbed. This fact has led to the establishment of the protected Sierra de Baza Natural Park in 1987.

Measurement of habitat features

At each sampling site, habitat structure was measured following a modification of the method described by Wiens and Rotenberry (1981). Horizontal plant cover and vertical plant complexity were analyzed. Two 50-m transects were established at each sampling site, noting the type of contacts (bare ground, stones, leaf litter, shrubs, herbs, or trees) beneath a pole (250 cm height) and the substrate at 2 points right and left of the bar at 1-m intervals. Total plant cover at each site was expressed as a percentage of contacts with vegetation. Also, plant cover (percentage) at different 10-cm-height intervals, from 0-10 cm to 250 cm and above, was estimated at each of the contacts mentioned above. Therefore, twenty-six data points of plant cover at different vertical intervals were estimated at each contact (total number of data points for each site was then 5200). Mean plant cover at each interval was calculated for each of the sampling sites, and then we applied Shannon's H' index of diversity (Shannon and Weaver 1949) to the data as an estimate of the vertical complexity of vegetation.

Detailed description of sampling sites

Nine sampling sites were selected according to elevation and habitat type, including different vegetation successional series (Table 1). For details on plant communities and vegetation types see Gómez-Mercado and Valle-Tendero (1988).

—SB1. Rambla del Chopo. Located at 1120 m on the northern slope of the Sierra de Baza, this site has a total plant cover of 60.0%. It is a dense scrubland habitat of *Quercus coccifera* L., *Juniperus oxycedrus* L., *Rosmarinus officinalis* L., and *Stipa* spp., shrubs occupying 40.5% of the area. Some oaks (*Quercus rotundifolia* Lam.) cover 7.5% of the total area, while the herbaceous layer covers 17.0%.

—SB2. Rambla de Ceuta. Also on the northern slope and located at 1200 m, site SB2 is an oak (*Quercus rotundifolia* Lam.) and pine (*Pinus halepensis* Miller) forest habitat, with a total plant cover of 45.5%. Trees cover 17.0% of the area, while shrub cover reaches 27.5% (*Stipa* spp., *Rosmarinus*

Table 1. List of the sampling sites, indicating elevation (m), vegetation type, plant cover (%), vertical complexity (V. complex.) of vegetation (see "Methods" for details), type of habitat and abundance (Ab.), species richness (Sp. R.), and H' diversity of dung beetles at each site

Locality	Elevation	Vegetation	Plant cover	V. complex.	Habitat	Ab.	Sp. R.	H'
SB1	1120	MSCR	60.0	2.52	HIGH	28	8	1.68
SB2	1200	OFOR	45.5	2.80	HIGH	19	5	1.69
SB3	1400	PFOR	58.0	3.10	HIGH	9	4	1.40
SB4	1520	MSCR	72.5	2.28	MEDIUM	18	4	1.27
SB5	1750	PFOR	67.5	2.77	HIGH	119	12	1.34
SB6	2150	PAST	89.5	1.46	LOW	135	14	2.40
SB7	2200	PFOR	93.5	2.10	MEDIUM	110	13	2.54
SB8	1840	MSCR	76.0	2.37	MEDIUM	138	14	2.34
SB9	1640	MSCR	61.5	1.93	LOW	54	10	2.22

MSCR: Mediterranean scrublands; OFOR: oak forest; PFOR: pine forest; PAST: pasture.

officinalis L., *Thymus* spp., and *Juniperus oxycedrus* L. being the most abundant species). The herbaceous layer covers only 5.5% of the area.

—SB3. Cortijo de Narváez. This site is located at 1400 m on the northern slope. Total plant cover reaches 58.0%. It is a dense pine forest (*Pinus halepensis* Miller) in which trees cover 35.0% of the area, with shrub layer being reduced (13.0%). It is also remarkable that 37.5% of the total area is bare ground.

—SB4. La Canaleja. Located at 1520 m, on the northern slope of the Sierra de Baza, this site is a scrubland on which plant cover reaches 72.5%. Shrubs cover 43.5% (*Rosmarinus officinalis* L. and *Juniperus oxycedrus* L. being the most abundant species), while the herbaceous layer occupies 46.5% of the area. No trees are present at this site.

—SB5. Umbría de los Perendengues. This site is located at 1750 m, on the northern slope. A dense pine forest (*Pinus halepensis* Miller) covers 24.0% of the area, while the shrub layer occupies 34.5% (mainly *Erinacea anthyllis* Link). Total plant cover reaches 67.5%).

—SB6. Los Prados del Rey. This sampling site is located at 2150 m, and is an open habitat where high-mountain pastures with low vertical development are well represented, with the herbaceous layer covering 62.5% (the main species being *Festuca iberica* Hackel, *Leontodon carpetanus* Lange, *Plantago subulata* L., and *Carex ovalis* Good). Shrubs cover 44.0% of the area (*Juniperus communis* L. *hemisphaerica* (K. Presl) and *J. sabina* L.), trees being virtually absent. Total plant cover reaches 89.5%.

—SB7. Near Calar de Santa Bárbara. Located near the top of Sierra de Baza (2200 m), this site is characterized by its high plant cover (93.5%). It is a rather open pine forest (*Pinus nigra* Arnold *salzmannii* Dunal), covering 25.5% of the total area, but a shrub layer of *Juniperus sabina* L. and *J. communis* L. *hemisphaerica* (K. Presl) is also well represented (47.5%).

—SB8. Puerto de los Tejos. This site, located at 1840 m on the southern slope, is a Mediterranean scrubland in which total plant cover reaches 76.0% of the area. A well-developed herbaceous layer is remarkable (65.5%), whereas shrubs cover 24.5% (mainly *Berberis hispanica* Boiss & Reuter and *Prunus* spp.). Trees are scarce, with pines (*Pinus halepensis* Miller) covering 7.0%.

—SB9. Charches. Also on the southern slope, this site is located at 1640 m and forms a rather open Mediterranean scrubland. Total plant cover is 61.5%; trees are almost absent (1% coverage), while shrubs occupy 24.5% (mainly *Stipa* spp. and *Thymus* spp.). The herbaceous layer represents 43.0% of the total area.

From plant cover and vertical complexity data, we ranked the sampling sites into 3 categories, according to several cut-off values that coincide with the 3 major habitat types described above. The first category (HIGH) included those sites in which vertical complexity was higher than 2.5 (SB1, SB2, SB3, and SB5); these sites are mainly forests (SB2, SB3, and SB5), but a dense scrubland (SB1) is also represented. The 2nd category (MEDIUM) was defined for sites with complexity values ranging between 2.0 and 2.5; this group included 2 scrublands (SB4 and SB8) and a rather open pine forest (SB7). The 3rd category (LOW) was defined as including sites with a complexity lower than 2.0, that in the study area were represented by an open Mediterranean scrubland with little vertical development (SB9) and an open pasture (SB6) (Table 1).

Sampling methods

Field work was carried out from June 1994 to February 1995. To sample coprophagous beetles, we used dung-baited pitfall traps of the bait-surface-grid type, a method established as one of the most efficient for these purposes (Lobo et al. 1988, Veiga et al. 1989). Traps were baited with 200 g of cattle dung and contained 20 cm^3 of a preservation solution (chloral hydrate 10 g/l). Each 2 weeks, two traps were placed separately at each sampling location, 4 m from each other, and were removed after 48 h. The location of each trap remained constant over the entire sampling period. The number of traps we used ensured an adequate pool of data, despite accidental trap losses, for statistical analysis. In fact, trap loss was high due to climatic factors or animals. The total number of traps analyzed was 296.

Data analysis

The relationships between plant cover or plant complexity and elevation were analyzed by means of Spearman rank correlation. Similarly, the relationships between mean abundance, species richness, or diversity per sample (1 individual trap) and elevation were examined. Faunistic turnover among assemblages belonging to the 4 different habitat types was measured as a proportion (percentage) of shared species between habitats, and also by means of the Morisita-Horn index of similarity modified by Wolda (Magurran 1988). Although new methods have been described to quantify faunistic

turnover (see for example Cody 1993 and its limitations in Halffter 1998), the Morisita-Horn index is one of the most powerful measurements of similarity between quantitative inventories (Magurran 1988).

Ecological diversity of scarabaeoid dung beetles has been estimated in 2 ways: species richness, following Gaston (1996) and Halffter (1998), and H' diversity (Shannon and Weaver 1949). Non-parametric statistics have been used because of the lack of normality of data distributions and the different number of samples to be compared. Spearman rank correlation was utilized to compare plant cover and complexity with elevation and for comparing abundance and diversity at different sites. Habitat selection (only for those species with 15 or more individuals) was analyzed using non-parametric statistics (Mann Whitney U test, as recommended by Potvin and Roff 1993), as well as comparisons of species richness and H' diversity between habitats.

RESULTS

Plant cover and vertical plant complexity values are shown in table 1 for each sampling site. Plant cover was positively correlated with elevation (R = 0.90; p = 0.0009; Spearman rank correlation), while a negative, marginally significant, correlation between vertical plant complexity and elevation occurred (R = −0.633; p = 0.067; Spearman rank correlation). Therefore, habitat tends to be less complex and be more covered by vegetation at high-elevation sites.

The community of scarabaeoid dung beetles in Sierra de Baza comprised 33 species belonging to the families Scarabaeidae, Aphodiidae, Geotrupidae and Trogidae, eight of them with abundances greater than 15 individuals (Appendix 1; see also Romero-Alcaraz et al. 1998). The sampling effort was adequate to correctly describe the community: near 90% of the expected species in the area were caught with the pitfall traps (Colwell 1997).

Both mean abundance and mean H' diversity per sample (1 individual trap) were positively correlated with elevation (R = 0.836; p = 0.004 and R = 0.700; p = 0.035; Spearman rank correlation), but no correlation occurred between elevation and mean species richness per sample (R = 0.516; p = 0.154; Spearman rank correlation).

Composition of assemblages in each habitat type was rather different from the others: similarity was generally low; the value of Morisita-Horn index varied from 0.33 between medium- and high-complexity habitats (39.28% of shared species),

to 0.56 between high- and low-complexity habitats (35.71% of shared species), and 0.88 between low- and medium-complexity habitats (51.85% of shared species).

In the entire assemblage, mean abundance, species richness, and H' diversity of beetles per sample were lower in high-complexity sites, although no differences were detected between medium- and low-complexity sites (Fig. 1). Members of the Aphodiidae were more abundant in low-complexity sites, while no selection was detected in the case of the Scarabaeidae (Table 2). Mean species richness was significantly greater in low-complexity sites in
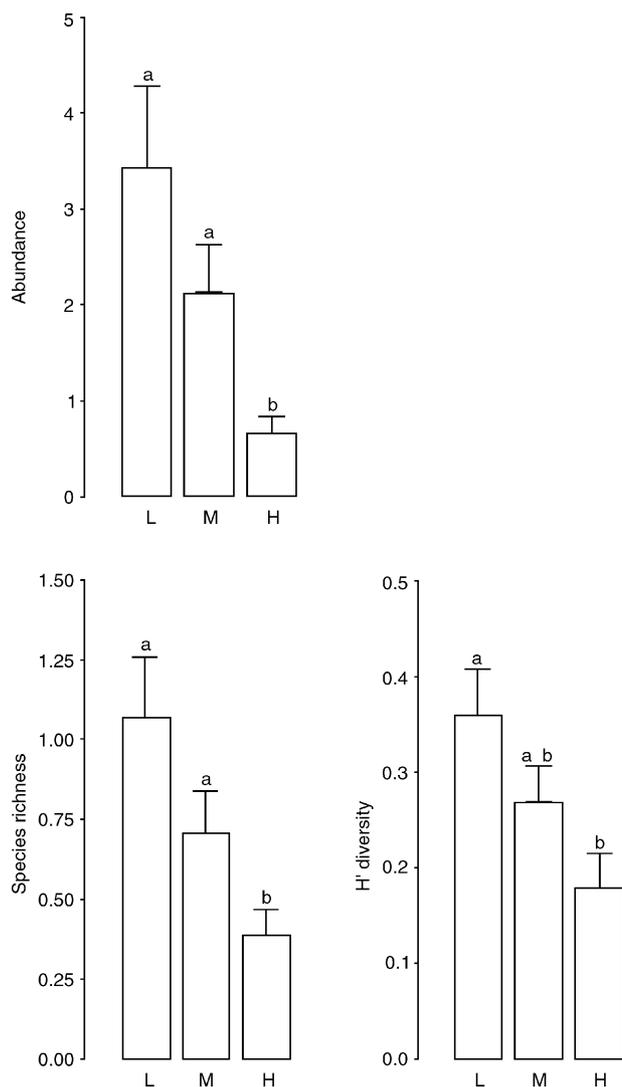

Fig. 1. Mean abundance, species richness, and diversity (H' index) of scarabaeoid dung beetles per sample ± SE in each habitat type defined in the text. Different letters indicate a significant difference (p < 0.01, by Mann Whitney U test). L: low complexity of habitat; M: medium complexity; H: high complexity.

Table 2. Habitat selection of the most abundant species collected and of the Scarabaeidae, Aphodiidae, and total Scarabaeoidea. Mean abundance per trap ± SE is shown. Different letters in a row indicate a significant difference (by Mann-Whitney U test, $p < 0.01$)

	Low $n = 70$	Medium $n = 105$	High $n = 121$
Aphodius affinis Panzer	0.10 ± 0.04[a]	0.10 ± 0.05[a]	0[b]
Aphodius distinctus (Müller)	0.66 ± 0.32[a]	0.22 ± 0.11[a,b]	0.07 ± 0.04[b]
Aphodius foetidus (Herbst)	0.29 ± 0.12[a]	0.38 ± 0.21[a,b]	0.01 ± 0.00[b]
Onthophagus punctatus (Illiger)	0.06 ± 0.03[a]	0[b]	0.22 ± 0.08[a]
Onthophagus vacca (L.)	0.11 ± 0.06	0.13 ± 0.05	0.02 ± 0.01
Onthophagus lemur (F.)	0.74 ± 0.46	0.23 ± 0.10	0.25 ± 0.07
Euonthophagus gibbosus (Scriba)	0.90 ± 0.44[a]	0.73 ± 0.22[a]	0.03 ± 0.02[b]
Euonthophagus amyntas (Olivier)	0.23 ± 0.14[a]	0.05 ± 0.03[a,b]	0.01 ± 0.00[b]
Scarabaeidae	2.55 ± 0.94	1.26 ± 0.37	0.60 ± 0.15
Aphodiidae	1.11 ± 0.34[a]	0.88 ± 0.29[b]	0.11 ± 0.04[c]
Total	3.67 ± 1.06[a]	2.13 ± 0.57[a]	0.71 ± 0.16[b]

the case of the Aphodiidae, while mean H' diversity was lowest in sites of high plant complexity (Table 3). Although a similar pattern occurred among the Scarabaeidae, differences were not significant (Table 3).

In general, species selected sites of low or medium complexity, such that high-complexity sites had the lowest abundances (Table 2). Only *Onthophagus punctatus* (Illiger) was more abundant in sites where complexity was higher, while no significant selection was shown in the cases of *O. vacca* (L.) and *O. lemur* (F.) (Table 2).

DISCUSSION

Elevation is an important factor influencing community structure, abundance, and diversity, with these often being negatively correlated with elevation (MacArthur 1972, Begon et al. 1986, McCoy 1990, Stevens 1992, Rahbek 1995). Lower productivity at higher elevations has been argued to cause such declines in abundance and diversity (Lawton et al. 1987), although no general pattern can be defined (Colwell and Hurtt 1994, Rahbek 1995). Nevertheless, in this work, both abundance and H' diversity were positively correlated with elevation. Changing habitat features along the elevational gradient probably determine the distribution of populations: Sierra de Baza has been managed for centuries; sites at low- and mid-elevations are those at which deforestation and recent afforestation practices were more intense. High-elevation sites remain less modified, corresponding, in general, with more open habitats than those in the lower part of the gradient. But even

those sites at the top of the gradient are usually used as pastures for livestock, mainly sheep (Muñoz 1992), in the spring and the summer, a period during which most scarabaeoid dung beetles are active as adults in the study area (Romero-Alcaraz et al. 1998). These circumstances may become important in determining the spatial distribution of dung beetles along elevational or habitat gradients: elevation itself does not explain the patterns of abundance of species and diversity variations in the communities, but habitat type is also remarkable. Hence, although habitats vary with elevation, these are transformed to a large extent by man-induced changes in the Sierra de Baza; these factors are probably significant for explaining the current structure of scarabaeoid dung beetle assemblages at different sites.

In general, scarabaeoid dung beetle communities were more abundant and diverse in low-com-

Table 3. Mean species richness and H' diversity per sample ± SE in each habitat for the families, Scarabaeidae and Aphodiidae. Letters indicate habitats for which differences were significant (by Mann-Whitney U test, $p < 0.05$)

	Species richness		
	Low	Medium	High
Scarabaeidae	0.67 ± 0.17	0.47 ± 0.10	0.30 ± 0.06
Aphodiidae	0.81 ± 0.30[a]	0.28 ± 0.05[b]	0.09 ± 0.03[c]

	H' diversity		
	Low	Medium	High
Scarabaeidae	0.12 ± 0.03	0.08 ± 0.01	0.05 ± 0.01
Aphodiidae	0.02 ± 0.01[a]	0.04 ± 0.01[a]	0[b]

plexity habitats. Dung beetles are in general well adapted for the olfactory location of resources (Ridsdill-Smith 1991), with dung particles suspended in the air acting as a stimulus for flying to the source. Such particles spread more efficiently through open habitats, where odor transmission is not prevented. In addition, the radiant energy level at the soil surface, which is greater in open habitats, is relevant for flight activity of dung beetles (Lobo et al. 1998), open habitats being therefore more adequate than closed habitats for coprophagous insects (Lumaret 1983). In relation with these facts, species generally selected open habitats, with the most abundant species also occurring in complex habitats, although abundance was lower in those biotopes, as was the case of *Onthophagus lemur* (F.) , *O. vacca* (L.), *Euonthophagus gibbosus* (Scriba), *E. amyntas* (Olivier), *Aphodius foetidus* (Herbst), and *A. distinctus* (Müller).

The Aphodiidae and Scarabaeidae considered separately showed different patterns: the Aphodiidae selected open habitats, probably because of the similarity of ecological and trophic requirements for most species: they generally are of small size and engage in endocoprid nesting (Cambefort and Hanski 1991). Although members of the Scarabaeidae were more abundant in open habitats, they showed no significant habitat selection. This is probably a consequence of the existence of several species having different requirements: two out of the 5 most abundant Scarabaeidae species (*Euonthophagus gibbosus* (Scriba) and *E. amyntas* (Olivier)) selected open ha-bitats, thus following the general pattern, while 1 species, *O. punctatus* (Illiger), selected closed habitats, as was previously recorded (Martín-Piera 1984), due to its association with rabbit latrines in oak forests (Sandoval and Ávila 1991, Sánchez-Piñero and Ávila 1991). Lastly, another 2 species, *Onthophagus vacca* (L.) and *O. lemur* (F.), showed no habitat selection, which probably reflects their more ubiquitous and generalist character (Martín-Piera 1984). The fact that these 2 species comprised 34.2% of all individuals of Scarabaeidae collected probably determined the lack of habitat selection by the family when considering all species together.

Other scarce species, like *O. ruficapillus* Brulle, *O. merdarius* (Chevrolat), or *Aphodius quadrimaculatus* L., all usually associated with open habitats (Dellacasa 1983, Martín-Piera 1984), occurred in the most-complex habitats. But for these species, as well as for others more abundant in open habitats like *Scarabaeus puncticollis* Latreille, *Gymnopleurus flagellatus* (F.), and *Onthophagus similis* (Scriba),

analyses were not possible due to their low abundance.

Different habitat selection by species and the scarcity of some of them which were present only in 1 of the 3 habitat types appear to be responsible for the low similarity among assemblages. So we can conclude that, in addition to positive correlations occurring between elevation and abundance or diversity of scarabaeoid dung beetles, habitat type appears to be crucial in determining both composition and abundance, and diversity of scarabaeoid dung beetles, those sites with open biotopes being the ones in which communities are more abundant and diverse. Landscape heterogeneity is a common feature of Mediterranean mountain ecosystems, but also centuries of human activities in the area have contributed to the current picture of heterogeneity, since most parts of the Sierra de Baza have suffered some degree of management or transformation. The existence of different patterns of habitat selection within a rather homogeneous guild, as scarabaeoid dung beetles, probably reflects the importance of maintaining high landscape heterogeneity in order to preserve beetle diversity in a protected natural area like Sierra de Baza.

REFERENCES

Anderson JM, MJ Coe. 1974. Decomposition of elephant dung in an arid, tropical environment. Oecologia (Berl.) **14:** 111-125.

Ávila JM, A Fernández-Sigler. 1988. Comportamiento frente a varias variables ecológicas de las comunidades de escarabeidos coprófagos en prado (Sierra de Alfacar, Granada) (Coleoptera, Scarabaeoidea). Actas III Congreso Ibérico Entomología, pp. 715-724.

Begon M, JL Harper, CR Townsend. 1986. Ecology. Individuals, populations and communities. Oxford: Blackwell Scientific Publications.

Cambefort Y, I Hanski. 1991. Dung beetle population biology. *In* I Hanski, Y Cambefort, eds. Dung beetle ecology. Princeton: Princeton Univ. Press, pp. 36-50.

Cody ML. 1993. Bird diversity components within and between habitats in Australia. *In* RE Ricklefs, D Schluter, eds. Species diversity in ecological communities: historical and geographical perspectives. Chicago: Univ. of Chicago, pp. 147-158.

Colwell RK. 1997. EstimateS: statistical stimation of species

richness and shared species from samples. Version 5. User´s Guide and application available at: http://viceroy.eeb.uconn.edu/estimates

Colwell RK, GC Hurtt. 1994. Nonbiological gradients in species richness and a spurious Rapoport effect. Am. Nat. **144:** 570-595.

Dellacasa G. 1983. Sistematica e nomenclatura degli Aphodiini italiani (Coleoptera Scarabaeidae: Aphodiinae). Monografie I. Torino: Museo Regionale di Scienze Naturali, pp. 1-465.

Desiére M. 1987. Écologie des coléoptères coprophiles en prairies pâturées et en forêt. Ph.D. dissertation. Univ. of Lieja, Belgium.

Gaston KJ. 1996. Species richness: measure and measurement. *In* KJ Gaston, ed. Biodiversity. A biology of numbers and difference. Oxford: Blackwell Science Ltd., pp. 77-113.

Giller PS, BM Doube. 1994. Spatial and temporal co-occurrence of competitors in Southern African dung beetle communities. J. Anim. Ecol. **63:** 629-643.

Gómez-Mercado F, F Valle-Tendero. 1988. Mapa de vegetación de la Sierra de Baza. Granada: Univ. de Granada Press.

Halffter G. 1998. A strategy for measuring landscape biodiversity. Biol. Intl. **36:** 3-17.

Hanski I. 1987. Colonization of ephemeral habitats. *In* 26th symposium of the British ecological society. London: Blackwell Scientific Publications, pp. 155-185.

Hirschberger P, T Bauer. 1994. The coprophagous insect fauna in sheep dung and its influence on dung disappearance. Pedobiologia **38:** 375-384.

Koskela H. 1972. Habitat selection of dung-inhabiting Staphylinids (Coleoptera) in relation to age of the dung. Ann. Zool. Fennici **9:** 156-171.

Koskela H, I Hanski. 1977. Structure and succession in a beetle community inhabiting cow dung. Ann. Zool. Fennici **14:** 204-223.

Landin J. 1967. On the relationship between the microclimate in cow droppings and some species of *Sphaeridium* (Col. Hydrophilidae). Opusc. Entomol. **32:** 207-212.

Lawton JH, M MacGarvin, PA Heads. 1987. Effects of altitude on the abundance and species richness of insect herbivores on bracken. J. Anim. Biol. **56:** 147-160.

Lobo JM. 1991. Coleópteros coprófilos, temperatura ambiental y pérdidas de peso en heces de vacuno (Coleoptera). Elytron **5:** 257-259.

Lobo JM, JP Lumaret, P Jay-Robert. 1998. Sampling dung beetles in the French Mediterranean area: effects of abiotic factors and farm practices. Pedobiologia **42:** 252-266.

Lobo JM, F Martín-Piera, CM Veiga. 1988. Las trampas pitfall con cebo, sus posibilidades en el estudio de Scarabaeoidea (Col.). I. Caracteristicas determinantes de su capacidad de captura. Rev. Ecol. Biol. Sol. **25:** 77-100.

Lumaret JP. 1983. Structure des peuplements de Coprophages Scarabaeidae en région méditerranéenne française: relation entre les conditions écologiques et quelques paramétres biologiques des espècies. Bull. Soc. Entomol. Fr. **88:** 481-495.

MacArthur RH. 1972. Geographical ecology: patterns in the distribution of species. New York: Harper & Rowe.

Magurran AE. 1988. Ecological diversity and its measurement. Princeton University Press.

Martín-Piera F. 1984. Los Onthophagini ibero-baleares (Col., Scarabaeoidea). II. Corología y autoecología. Eos **60:** 101-173.

McCoy ED. 1990. The distribution of insects along elevational gradients. Oikos **58:** 313-322.

Medina J, M Chirosa. 1992. Caracterización fisica del Parque Natural Sierra de Baza. *In* Junta de Andalucía, ed. Parque Natural Sierra de Baza, pp. 18-30.

Menéndez R, D Gutiérrez. 1996. Altitudinal effects on habitat selection of dung beetles (Scarabaeoidea: Aphodiidae) in the northern Iberian peninsula. Ecography **19:** 313-317.

Mohr CO. 1943. Cattle droppings as ecological units. Ecol. Monogr. **13:** 275-309.

Muñoz A. 1992. Situación y perspectivas socioeconómicas del área de influencia del Parque Natural de la Sierra de Baza. *In* Junta de Andalucia, ed. Parque Natural Sierra de Baza, pp. 84-110.

Potvin C, DA Roff. 1993. Distribution-free and robust statistical methods: viable alternatives to parametric statistics? Ecology **74:** 1617-1628.

Rahbek C. 1995. The elevational gradient of species richness: a uniform pattern? Ecography **18:** 200-205.

Ridsdill-Smith J. 1991. Competition in dung-breeding insects. *In* WJ Bailey, J Ridsdill-Smith, eds. Reproductive behaviour of insects. Individuals and populations. London: Chapman and Hall, pp. 264-292.

Romero-Alcaraz E, JM Ávila, F Sánchez-Piñero. 1998. Inventario faunístico y corología de los escarabeidos coprófagos de la Sierra de Baza (Granada, Sureste de la Península Ibérica). Zool. Baetica **9:** 47-67.

Sandoval P, JM Ávila. 1991. Autoecología de las especies de escarabeidos coprófagos (Col., Scarabaeoidea) de los excrementos de conejo (*Oryctolagus cuniculus* L.). Boll. Mus. Reg. Sci. Nat. Torino **9:** 375-389.

Sánchez-Piñero F, JM Ávila. 1991. Análisis comparativo de los Scarabaeoidea (Coleoptera) coprófagos de las deyecciones de conejo [*Oryctolagus cuniculus* (L.)] y de otros mamiferos. Estudio Preliminar. Eos. **67:** 23-24.

Shannon CE, W Weaver. 1949. The mathematical theory of communication. Chicago: University of Illinois Press.

Sowig P, T Wassmer. 1994. Resource partitioning in coprophagous beetles from sheep dung: phenology and microhabitat preferences. Zool. Jb. Syst. **121:** 171-192.

Stevens GC. 1992. The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. Am. Nat. **140:** 893-911.

Veiga CM, JM Lobo, F Martin-Piera. 1989. Las trampas pitfall con cebo, sus posibilidades en el estudio de las comunidades coprófagas de Scarabaeoidea (Col.). II. Análisis de efectividad. Rev. Ecol. Biol. Sol. **26:** 91-109.

Wiens JA, JT Rotenberry. 1981. Habitat association and community structure of birds in shrubsteppe environments. Ecol. Monogr. **51:** 21-41

Appendix 1. List of all species of scarabaeoid dung beetles collected in the study area, indicating the pooled abundance, species richness, and H' diversity in each habitat type

	Low	Medium	High	Total
Family Trogidae	—	2	9	11
Trox perlatus Geof.	—	2	9	11
Family Scarabaeidae	179	134	73	386
Scarabaeus (Scarabaeus) sacer L.	1	—	—	1
Scarabaeus (Scarabaeus) typhon Fisc.Wald.	1	—	1	2
Scarabaeus (Ateuchetus) puncticollis Latreille	9	—	—	9
Gymnopleurus flagellatus (F.)	10	—	—	10
Caccobius schreberi (L.)	1	—	—	1
Euonthophagus gibbosus (Scriba)*	63	77	4	144
Euonthophagus amyntas (Olivier)*	16	5	1	22
Onthophagus lemur (F.)*	52	24	31	107
Onthophagus (Palaeonthophagus) similis (Scriba)	5	8	—	13
Onthophagus (Palaeonthophagus) fracticornis (Preyssler)	2	2	—	4
Onthophagus vacca (L.)*	8	14	3	25
Onthophagus (Palaeonthophagus) ruficapillus Brulle	—	1	1	2
Onthophagus (Palaeonthophagus) merdarius (Chevrolat)	7	1	5	13
Onthophagus (Trichonthophagus) maki (Illiger)	—	2	—	2
Onthophagus punctatus (Illiger)*	4	—	27	31
Family Aphodiidae	79	112	18	209
Aphodius (Agrilinus) ibericus Harold	—	—	2	2
Aphodius (Agrilinus) constans Duftsmidt	—	—	1	1
Aphodius (Ammoecius) lusitanicus Erichson	2	2	—	4
Aphodius (Ammoecius) elevatus (Olivier)	—	6	—	6
Aphodius affinis Panzer*	7	11	—	18
Aphodius (Anomius) annamariae Baraud	—	11	—	11
Aphodius (Aphodius) fimetarius L.	—	8	—	8
Aphodius foetidus (Herbst)*	20	40	1	81
Aphodius (Calamosternus) granarius (L.)	1	5	2	8
Aphodius distinctus (Müller)*	47	27	8	82
Aphodius (Eurodalus) tersus Erichson	1	—	—	1
Aphodius (Melinopterus) sphacelatus (Panzer)	1	1	—	2
Aphodius (Phalacronothus) putoni Reitter	—	—	1	1
Aphodius (Phalacronothus) quadrimaculatus L.	—	—	1	1
Pleurophorus caesus (Creutzer)	—	1	2	3
Family Geotrupidae	—	1	5	6
Sericotrupes niger Marshan	—	1	—	1
Thorectes laevigatus F.	—	—	5	5
Total abundance	258	249	105	612
Species richness	20	21	18	33
H' diversity	2.24	2.29	2.16	2.58

*Species used for analysis of habitat selection.

海拔高度與棲所型式對南伊伯利亞半島糞金龜豐度與歧異度的影響

Eduardo Romero-Alcaraz[1]   José M. Ávila[1]

　　海拔高度與棲所型式是影響昆蟲群聚的兩個重要因素。本研究以陷阱捕捉法來測試海拔高度與棲所型式對伊伯利亞半島東南部糞金龜群聚的影響，並以棲所型式和海拔高度將傾向於棲所選汰型種類的歧異度加以量化。從我們的研究中得知，豐度與歧異度和海拔高度呈正相關，棲所型式和物種在群聚中的結構也有相關。一般而言，在整個集合體中，不同生物小種的相似程度低，特別是在棲所是開放型和封閉型之間。其中開放型具有較高的豐度與歧異度。雖然大多數的種類在封閉型棲所裏的豐度較低，一般性的種類則沒有選擇性上的偏好存在。因此，我們認為雖然糞金龜在開放型棲所裏較為適應生存，但是在不同集合體內不同族群的存在，或許反映出高異質性在維持糞金龜多樣性裏所扮演的重要角色。

關鍵詞：棲所選汰，糞金龜歧異度，海拔高度效應，金龜子科，牛糞金龜子科 。

[1]Departamento de Biologia Animal y Ecologia, Universidad de Granada, Campus de Fuentenueva, E-18071, Granada, Spain