A comparative discussion of trophic preferences in dung beetle communities

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A comparative discussion on trophic preferences in dung beetle communities.- Available information on trophic preferences of dung beetles (Scarabaeoidea) in different biogeographic regions is reviewed. Trophic resource partitioning in a dung beetle (Coleoptera, Scarabaeoidea) community in the «Parque Nacional de Doñana», Spain, was also studied, using nine different kinds of wild and domestic vertebrate excrement as trap bait. Undifferentiated attraction to human and herbivore faeces was noted. Human and domestic ungulate faeces was colonized by a richer fauna than that of wild herbivores, which was not the specialized trophic adaptation of any species. Although polyphagy is the most common feeding behaviour, the excrement of carnivores and other omnivores was hardly colonized. This pattern differs from that of other biogeographic regions. Negligible importance of the trophic dimension on the structure of these communities may be due to the early presence of man in the Palaearctic Region. Nevertheless, human interference alone cannot have led to an absence of true polyphagy (undifferentiated attraction to all kinds of faeces). Further research is suggested, aimed at determining whether observed resource partitioning in dung beetles communities is a consequence of human colonization or is a pre-Neolithic evolutionary event.

Key words: Dung beetles, Coleoptera, Scarabaeoidea, Trophic preferences, Resource partitioning, Ecological-historical causes.

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Introduction

The physical and chemical composition of herbivore faeces varies widely with the species (HANSKI, 1987), and even with season within the same species, as a function of pasture quality (GREENHAM, 1972; MATTHIESSEN, 1982; RIDSDILL-SMITH, 1986). Still greater variation occurs among the faeces of herbivores, omnivores and carnivores. In many cases it has been shown that dung beetles are attracted differently to different types of faeces (PAULIAN, 1943). It has been argued that trophic choice could play a role in determining the coexistence of species of a dung beetle community, and their resource partitioning.

Few studies have been made on the trophic preferences of the Palaearctic Region temperate biomes species, and these deal with the differential attraction of the food resources of no more than four mammal species (LANDIN, 1961; RAINIO, 1966; DESIÈRE & THOMÉ, 1977; LOBO, 1985; CARPANETO & PIATELLA, 1986; SÁNCHEZ-PIÑERO & ÁVILA, 1991). With the exception of the works by NIBARUTA et al. (1980) and NIBARUTA (1982), no joint study, using the faeces of both wild and domestic mammals, has been made in this region.

This paper attempts to determine whether differences correlated with faeces type exist in an Iberian dung beetle community. Results are compared with those previously obtained in the same and other biogeographic regions to: i) verify the importance of food preference results in resource partitioning and ii) provide material for a discussion, from a historical point of view, of the extent to which trophic preference may have conditioned the present composition of these communities.

Material and Methods

The study was carried out in or near a grove of holm oaks on the northern edge of 'Parque Nacional de Doñana' (one of the most important wildlife reserves in the Mediterranean area), within the locality of El Rocío, Huelva, UTM 29SQB2812 (Spain).

The sampling was taken in a clearing by means of 15 pitfall traps set out randomly on 60 x 40 m grid, average distance between traps of 10 m, left for 48 h (23-25 April, 1992).

The pitfall-traps were baited with approximately 1,000 g of fresh excrement (see LOBO et al., 1988; VEIGA et al., 1989), except in the case of lynx and fox faeces-baited traps (250 g were used), due to the scarcity of resources.

Nine kinds of excrement were used, from vertebrates that still live in the reserve, ranging from herbivore (cow, horse, deer and fallow deer); predominantly herbivore (wild boar); predominantly carnivore (lynx, fox); to omnivore (man, badger).

Two traps were baited with each type of faeces, except for those using faeces from lynx, fox and man (table 1).

There is evidence in favour of a density of two traps per site being adequate to have a good representation of the dung beetle community structure in the Mediterranean regions. Such a density ensures that about 53% of local spring species are captured (confidence intervals at 95% are 51.08-55.27%), these species representing 86% of total abundance and 85% of total biomass (Lobo & Lumaret, in preparation).

At the same time, samples were taken from one fresh cow-dung baited (1,000 g) pitfall trap, set for 48 h in each of the following eight park habitats: inter-sand-dune troughs devoid of vegetation ('corrales'); stationary dunes reforested with pines; marsh; original holm oak and cork oak wood; marsh-holm oak ecotone; scrub fringes of semi-permanent lagoons ('lucios'); stream bank primary and reforested woods (table 2).

The samples were examined to determine local fauna diversity, and to obtain an estimate of the abundance and habitat distribution of each species.

Results

The number of individuals of each species collected with each type of bait is shown in table 1. As figure 1 shows, faeces bait type fell into three groups, according to the number of species and individuals captured: group A, greatest richness and abundance (cow, human and one of the horse dung); group B, medium to high richness, lower abundance (three species of wild herbivore and another horse dropping trap); group C, very poor both in diversity and abundance (carnivores and badger). Total biomass (computations based on length-body weight regressions; LOBO, 1992, 1993) per group was also the greatest for group A (fig. 2).

Whittaker's plots of species abundance data (WHITTAKER, 1965) indicate: uneven distribution of abundance in the horse dropping community (fig. 3), giving low eveness and diversity values; a more even distribution of abundance and greater diversity, in cow, fallow deer and human dung beetle communities; fewer species, none dominant, in deer and wild boar, and thus high eveness and diversity values, along with an even species abundance figures.

Faunal similarity found in the different types of faeces was cluster analysed, using percent dissimilarity (PD) and UPGMA, flexible, weighted and unweighted centroid grouping strategies (LUDWIG & REYNOLDS, 1988). Dung beetle species
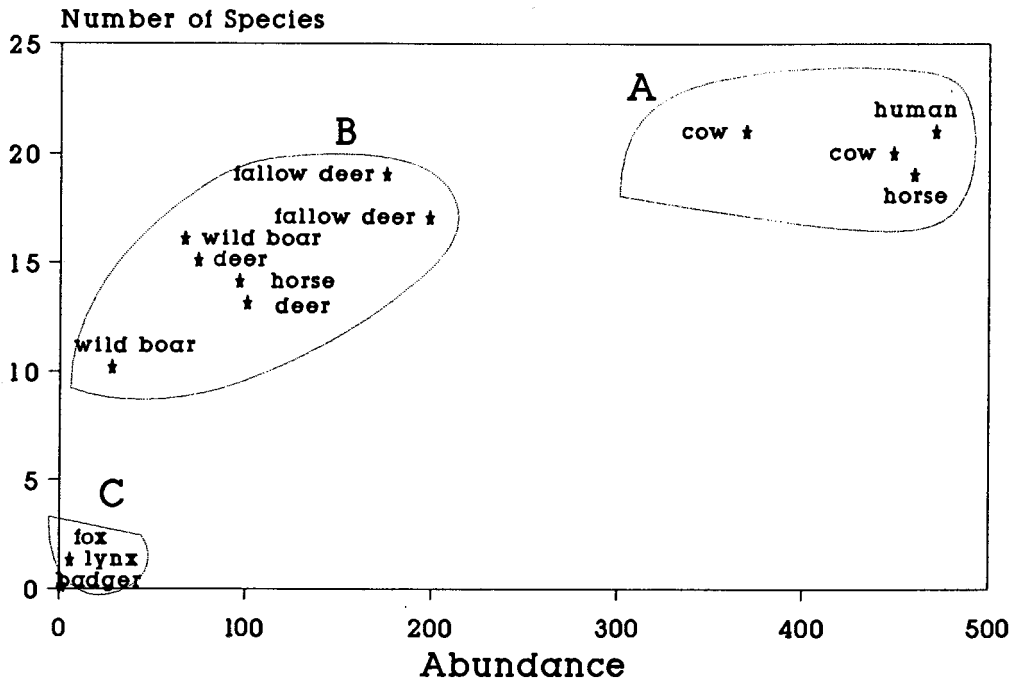

Fig. 1. Relationship between number of species and abundance for the 15 dung-baited pitfall traps belonging to nine different dung types.
Relación entre el número de especies y la abundancia para 15 trampas pitfall cebadas con nueve tipos diferentes de excrementos.

Species	H1	H2	C1	C2	W1	W2	Faeces B1	B2	D1	D2	F1	F2	L	Fo	Hu	Tot	Nb
Scarabaeus cicatricosus	1	1	0	0	1	0	0	0	1	0	0	1	0	0	9	14	0.09
S. sacer	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.07
Copris hispanicus	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	3	0.18
Euoniticellus fulvus	3	0	1	1	0	1	0	0	0	0	11	0	0	0	1	18	0.26
E. pallipes	0	1	1	3	1	9	0	0	1	5	9	10	0	0	1	41	0.39
Onitis belial	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.07
Bubas bison	0	0	0	1	0	0	0	0	0	0	0	0	0	0	4	5	0.03
B. bubalus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0.07
Onthophagus furcatus	2	2	1	8	1	0	0	0	0	2	2	3	0	0	3	24	0.49
O. maki	10	21	34	48	6	8	0	0	12	4	6	5	0	0	52	206	0.37
O. punctatus	2	1	0	0	0	0	0	0	1	0	0	0	0	0	1	5	0.22
O. similis	299	55	134	188	5	3	0	0	6	74	38	77	0	0	237	1116	0.42
O. opacicollis	97	11	58	82	3	7	0	0	10	0	23	29	0	0	63	383	0.42
O. taurus	0	2	9	15	3	8	0	0	6	3	17	19	0	0	6	88	0.44
O. vacca	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	3	0.18
Caccobius schreberi	15	3	1	20	0	2	0	0	6	2	11	13	0	0	18	91	0.50
Aphodius baraudi	4	0	2	5	3	4	0	0	4	2	0	0	0	0	11	35	0.37
A. erraticus	1	0	6	5	0	0	0	0	1	0	4	5	0	0	0	22	0.27
A. fimetarius	0	0	1	0	0	1	0	0	0	1	1	0	0	0	0	4	0.50
A. granarius	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	3	0.25
A. ictericus	0	0	12	3	0	0	0	0	0	0	2	0	0	0	0	17	0.11
A. immundus	1	1	3	3	0	2	0	0	0	0	3	2	0	0	1	16	0.44
A. lineolatus	7	0	35	8	0	0	0	0	1	3	16	4	0	0	4	78	0.30
A. lividus	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	0.21
A. longispina	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2	0.07
A. luridus	0	0	0	2	0	0	0	0	1	0	1	0	0	0	0	4	0.31
A. merdarius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	11	0.01
A. satellitius	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.07
A. scybalarius	0	0	5	9	0	2	0	0	2	1	4	1	0	0	5	29	0.35
A. striatulus	7	1	29	18	3	11	0	0	4	4	12	14	0	0	14	117	0.47
A. sturni	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	2	0.21
A. tersus	6	1	27	20	1	3	0	0	4	2	12	13	0	0	15	104	0.38
A. unicolor	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0.07
Thorectes hispanicus	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0.07
Typhaeus momus	2	2	2	4	0	1	0	0	0	0	0	2	1	1	13	28	0.21
Total abundance	461	103	365	445	27	64	0	0	61	104	174	201	1	1	470	2477	
Total no. species	19	14	21	20	10	16	0	0	16	13	19	17	1	1	21	35	
Total biomass	4.6	1.6	2.9	4.3	0.5	0.6	0	0	0.8	0.9	1.3	2.2	0.1	0.1	8.4	28.3	

Table 1. Dung beetles species caught with pitfall traps baited with faeces of : H. Horse; C. Cow; W. Wild boar; B. Badger; D. Deer; F. Fallow deer; L. Lynx; Fo. Fox; Hu. Human; Nb. Hurlbert's standardized niche breath (1978).
Inventario de coleópteros coprófagos capturados con trampas pitfall ceba-das con heces de: H. Caballo; C. Vaca; W. Jabalí; B. Tejón; D. Ciervo; F. Gamo; L. Lince; F. Zorro; Hu. Heces humanas; Nb. Amplitud de Nicho estandarizada de Hurlbert (1978).

found in cow, human, horse, and to a lesser degree, fallow deer dung, were very similar (fig. 4). Associated with them, fauna found in wild boar and deer were also similar. Only one species (*Typhaeus momus)* was not caught in any other bait type except in carnivore dung (lynx and fox). This clustering pattern was always independent of the grouping strategies used.

The null hypothesis of an equal probability of colonizing any faeces was estimated using a χ^2 test. Species abundance figures used were restricted to samples in which at least one beetle was caught (n = 13), thus excluding badger-faeces fauna figures. Excepting the case of *Aphodius immundus* Creutzer ($\chi^2 = 19.64$, $0.5 > P > 0.1$), all observed faeces abundance values differ significantly
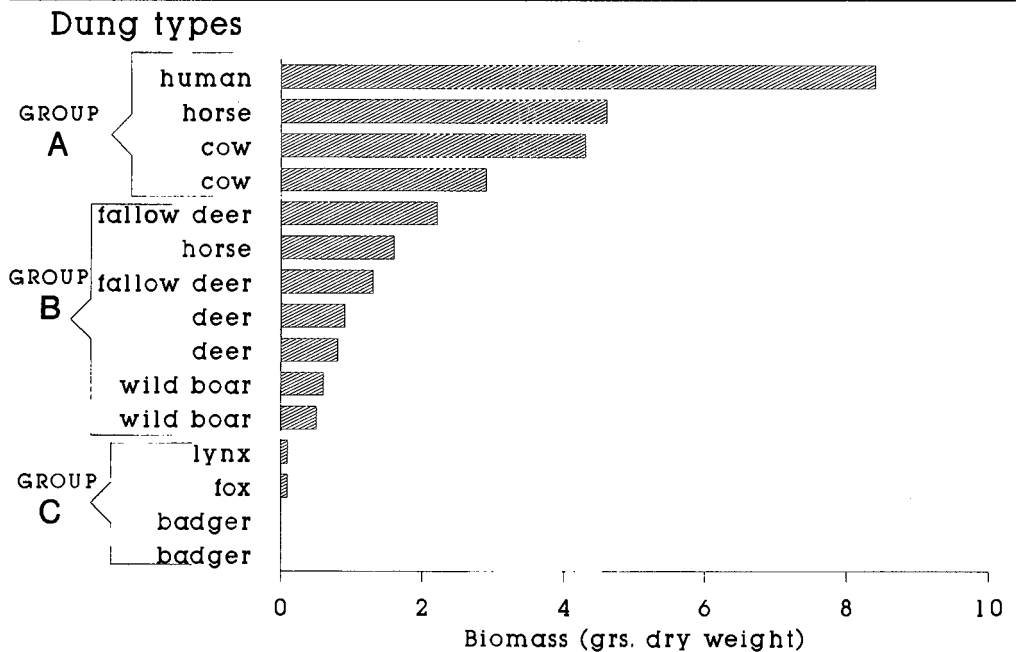

Fig. 2. Total biomass captured for the 15 dung-baited pitfall traps belonging to nine different dung types.
Biomasa total conseguida para las 15 trampas pitfall con nueve tipos diferentes de excrementos.

Tabla 2. Species inventory of dung beetles caught with pitfall traps baited with cow dung, in the Parque Nacional de Doñana, Huelva (Spain): 1. Sandy dunes; 2. Pine-reforested dunes; 3. Scrub; 4. Marsh-holm oak ecotone; 5. Marsh; 6. Holm oak and cork oak clearing; 7. Pine-reforested clearing; 8. Stream bank woods. Nb. HURLBERT's standardized niche breadth (1978).

Inventario de coleópteros coprófagos capturados con trampas pitfall cebadas con excrementos de vaca en el Parque Nacional de Doñana: 1. Dunas; 2. Dunas reforestadas con pinos; 3. Matorral; 4. Ecotono marisma-encinar; 5.Marisma; 6. Claro en bosque mixto de encinas y alcornoques; 7. Claro en pinar de repoblación; 8. Bosque de ribera; Nb. Amplitud de nicho estandarizada de HURLBERT (1978).
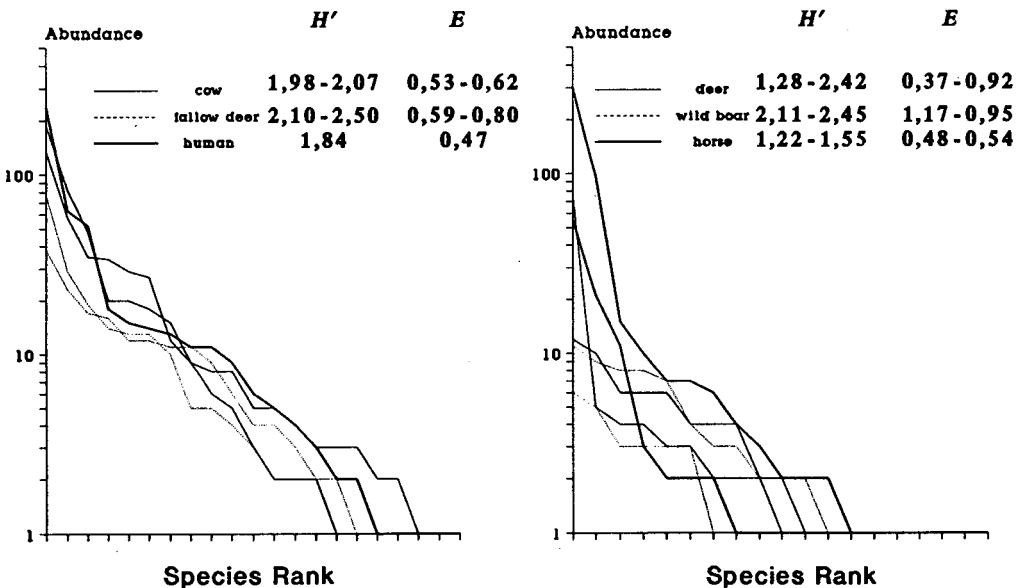

Fig. 3. WHITTAKER's plots of species abundance data (1965) for the six dung types most colonized: H'. Shannon's index of diversity; E. Evenness (Modified Hill's ratio, LUDWIG & REYNOLDS, 1988). Except for human faeces, the species abundance curve for every pair of dung baited traps, are plotted.

Curvas de especies-abundancia (WHITTAKER, 1965) de los seis tipos de excrementos más colonizados: H. Índice de diversidad de Shannon; E. Equitatividad (Ratio de Hill modificada, LUDWIG & REYNOLDS, 1988). Se han ilustrado las curvas de abundancia para cada par de trampas, excepto en las heces humanas.

| Species	1	2	3	4	5	6	7	8	Tot	Nb
					Sites					
Scarabaeus cicatricosus	13	122	243	49	0	0	7	0	434	0.20
S. sacer	12	6	11	3	1	0	0	0	33	0.39
Euoniticellus fulvus	0	0	1	12	3	1	3	0	20	0.25
E. pallipes	0	0	3	11	7	1	0	0	22	0.28
Onitis belial	0	0	0	3	0	1	0	0	4	0.14
Onthophagus furcatus	1	0	4	0	0	1	1	0	7	0.27
O. maki	1	15	156	41	0	34	12	3	262	0.26
O. punctatus	0	1	0	3	0	0	0	8	12	0.19
O. similis	0	2	23	273	0	134	13	4	449	0.21
O. opacicollis	0	0	0	3	3	58	2	1	67	0.10
O. taurus	3	34	178	38	6	9	6	4	278	0.23
O. vacca	0	0	0	11	4	2	1	0	18	0.23
Caccobius schreberi	0	0	0	5	3	1	7	0	16	0,33
Aphodius baraudi	5	18	12	3	0	2	1	0	41	0.37
A. erraticus	0	0	0	82	0	6	22	1	111	0.15
A. fimetarius	0	0	0	4	0	1	0	0	5	0.12
A. granarius	0	0	0	0	0	0	7	2	9	0.13
A. haemorrholdalis	0	0	0	2	1	0	0	0	3	0.17
A. ictericus	0	3	7	1	0	12	0	0	23	0.27
A. immundus	0	0	0	15	0	3	28	0	46	0.20
A. lineolatus	0	1	3	1	0	35	2	0	42	0.12
A. lividus	0	0	0	0	0	0	1	0	1	0.06
A. longispina	0	0	0	0	1	0	1	0	2	0.19
A. luridus	0	0	0	1	0	0	0	0	1	0.06
A. merdarius	0	0	0	0	0	0	1	0	1	0.06
A. satellitius	0	0	0	1	0	0	0	0	1	0.06
A. scybalarius	0	0	0	3	0	5	0	0	8	0.18
A. striatulus	12	9	182	23	16	29	4	0	275	0.21
A. sturmi	1	3	0	0	0	1	0	0	5	0.23
A. tersus	1	0	2	20	0	27	23	0	73	0.36
A. unicolor	0	0	0	0	0	0	47	0	47	0.06
Heptaulacus algarbiensis	0	0	1	0	0	0	0	0	1	0.06
Typhoeus momus	3	2	4	0	0	2	0	0	11	0.42
Trox cotodognanensis	0	1	0	0	0	0	0	0	1	0.06
Total abundance	52	217	830	608	45	365	189	23	2329	
Total number of species	10	13	15	24	10	21	20	7	34	

PD
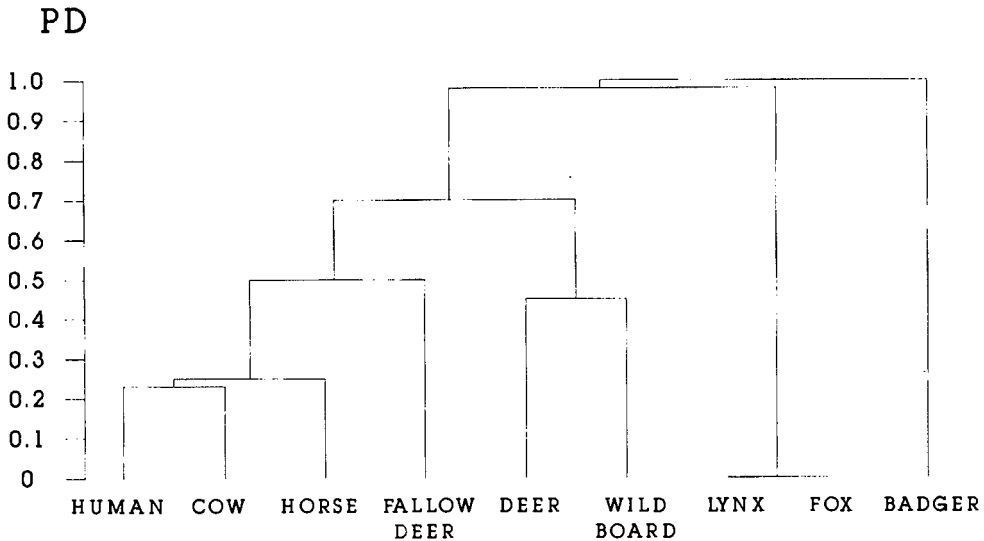
Fig. 4. Dendrogram of the clustering of nine dung types using the Percentage Dissimilarity (PD) as measure of resemblance and UPGMA as clustering strategy.

Dendrograma de similitud faunística entre los nueve tipos de excrementos. La medida de similitud es el Porcentaje de Disimilaridad (PD) y la estrategia de agrupamiento es UPGMA.

from values derived from equal probability hypothesis (P < 0.001 in all cases). Species trophic preference values can be determined from the ratio of individuals captured with a given faeces to total captures (fig. 5). Only in the cases of cow, human, horse and fallow deer faeces were species captured which accounted for more than 25% of the total.

Thirty-one species were attracted to group A faeces, 30 to group B, and only one to group C. Of the eight species captured in only one faeces group, seven consisted of three or fewer individuals, and may be considered incidental captures. Only the moderately abundant (n = 11) *A. merdarius* (Fabricius) was captured exclusively in group A. The number of individuals captured in group A and B was used to compare the average number of individuals per dung type for species in

both groups. Data from the 18 species with an abundance ≥ 13 were used. This figure is the minimum abundance of any species evenly distributed in every dung-baited trap, one beetle per trap. Species found in both groups with a significantly different average number of individuals per excrement were: *Onthophagus maki* (Illiger) (t = 3.61, 0.002 < P < 0.01), *O. similis* (Scriba) (t = 5.83, P < 0.001), *O. opacicollis* Reitter (t = 7.48, P < 0.001), *A. striatulus* Waltl (t = 2.35, P = 0.05), *A. tersus* Erichson (t = 2.86, P = 0.02) and *Typhaeus momus* (Olivier) (t = 2.31, P = 0.05). The figures for *A. scybalarius* (Fabricius) (t = 2.19) and *A. baraudi* Villareal (t = 2.15) were at the limit of statistical significance (t = 2.262, P = 0.05). The average number of individuals of all these species was greatest in group A, which means that around 40% of the sampled species were attracted
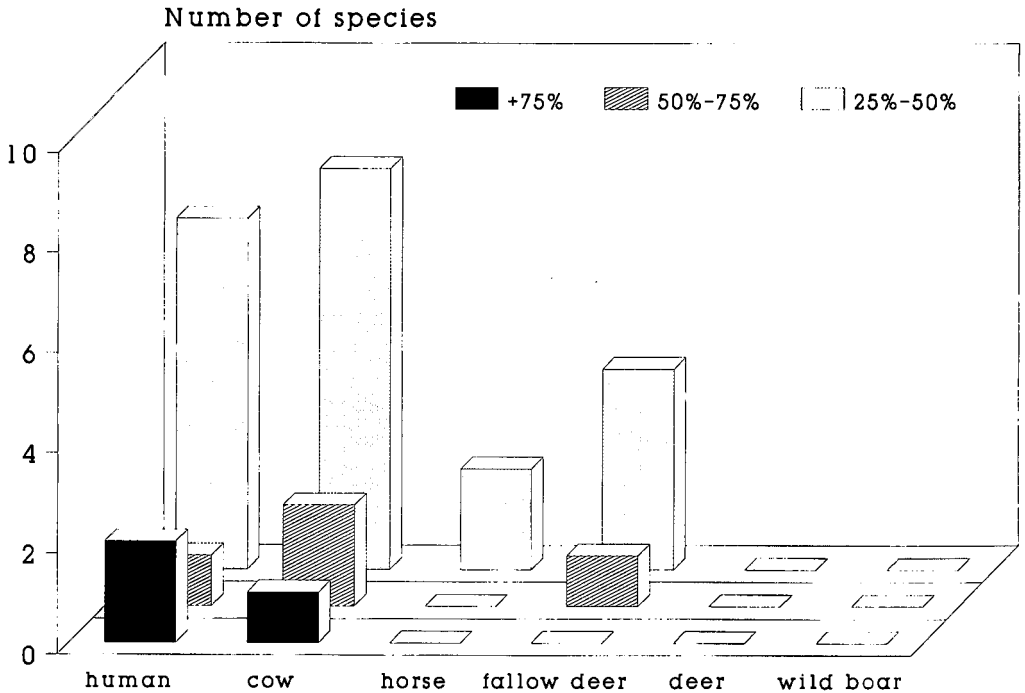
Number of species

Fig. 5. Number of species represented by more than 75%, between 50%-75% and between 25%-50% of total individuals in some of the six most colonized dung types.

Número de especies representadas por más del 75%, entre el 50 y el 75% y entre el 25 y el 50% del total de individuos en algunos de los seis tipos de excrementos más colonizados.

with greater frequency to cow, human and horse faeces.

The richness and abundance of species in the sampling from different habitats (table 2) was very similar to that of the different bait types (table 1). Of the 38 species captured, only seven (18%) did not belong to both samplings. All these seven species may be considered as incidental captures (three or fewer individuals). There is a highly significant correlation between the number of individuals of each species captured in the two samplings (r = 0.613, df = 29, P < 0.001). HURLBERT's standardized niche breadth (1978) was calculated using again the trophic and habitat data

of the 18 species with an abundance ≥ 13, as mentioned above (tables 1 and 2), giving uncorrelated values (r = -0.03, df = 16, NS). The mean trophic niche breadth (± S.E.) value (0.35 ± 0.03) was found to be rather higher than that of the mean habitat niche breadth (0.24 ± 0.02).

High species abundance values correlate with wide trophic niche breadths, while low values are uncorrelated (fig. 6A). Sixteen of the 18 species (n ≥ 13) were found in at least five faeces (simplifying the data by excluding the contribution from lynx, fox and badger). Only *A. erraticus* (L.) (n = 22) and *A. ictericus* (Laicharting) (n = 17) seemed to demonstrate a marked trophic predilection for cow dung.
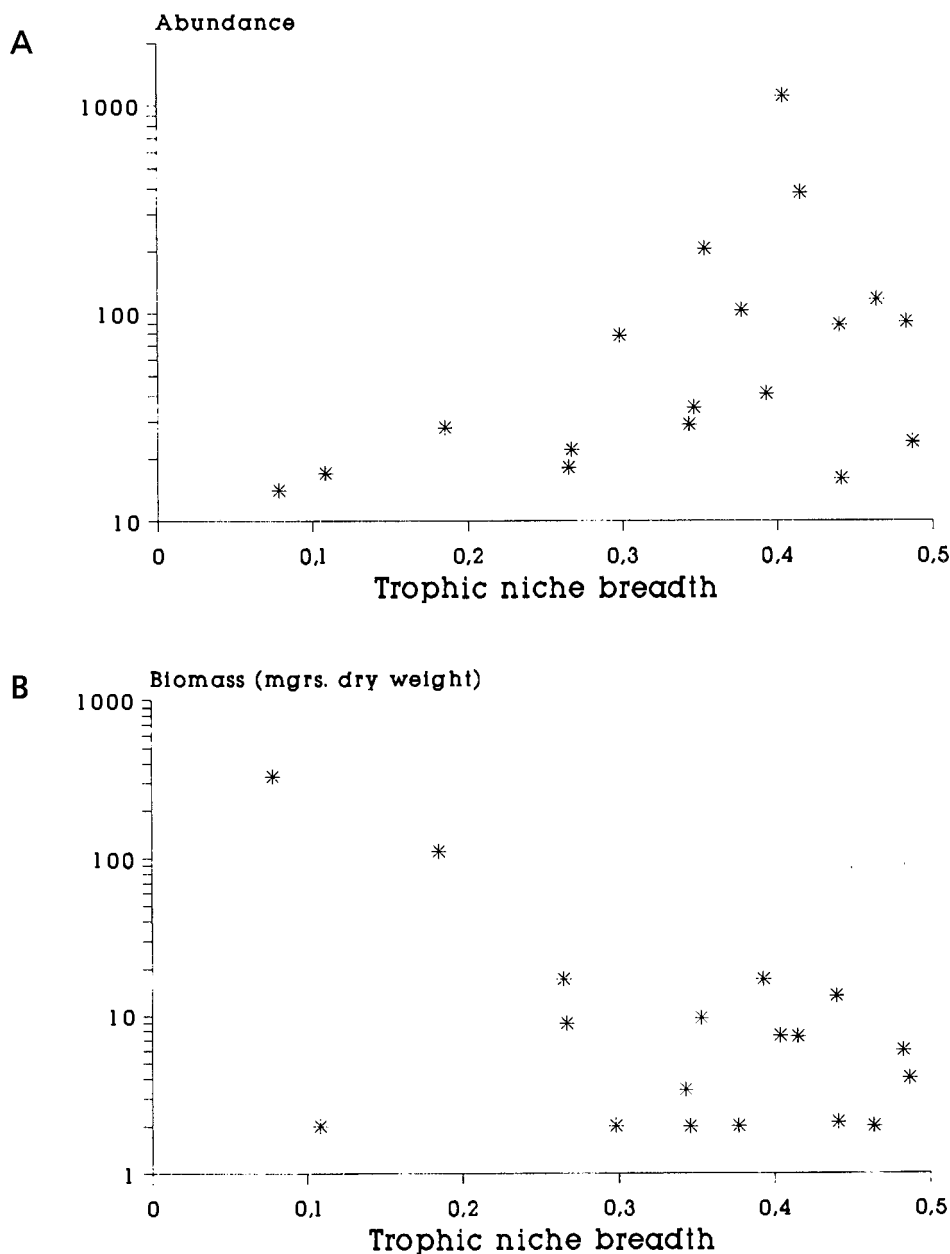
Fig. 6. Relationship between trophic niche breadth of species and its: A. Abundance; B. Dry weight. (Niche breadth measured with HURLBERT's standardized niche breadth, 1978).
Relación entre la amplitud de nicho trófico de las especies y su: A. Abundancia; B. Peso seco. (Amplitud de nicho calculada mediante el Índice de HURLBERT, 1978).

Table 3. Total abundance and total biomass for five trophic niche breath ranges (HURLBERT, 1978).
Abundancia total y biomasa total existente para cinco rangos de amplitud de nicho trófico (HURLBERT, 1978).

Trophic niche breadth ranges	Abundance	Biomass
0-0.09	14	4.62
0.1-0.19	45	3.14
0.2-0.29	118	0.66
0.3-0.39	415	3.05
0.4-0.50	1,835	13.15

There was no correlation between species dry weight and trophic niche breadth in which 18 species (fig. 6B), but it is interesting to note that *Scarabaeus cicatricosus* (ball roller) and *T. momus* (ball-carrier; see ZUNINO & PALESTRINI, 1986), the only large sized species, were among those three with the narrowest trophic niche breadth. While niche breadth gradually increased with total abundance, total captured biomass did not (table 3).

Discussion

A general review on trophic preferences of dung beetles

Species of Scarabaeidae in the tropics frequently show copro-necrophagous feeding habits (HANSKI, 1989; WALTER, 1983), and specialized trophic preferences predominantly occur (HALFFTER, 1959; HALFFTER & MATTHEWS, 1966). Carnivore dung fauna in such regions are made up of dung beetles attracted to carrion and herbivore dung (HANSKI, 1987). In Southeast Asian and South American tropical forest species are specialized in feeding on carrion or faeces, but about one half of these species make equal use of carrion and dung (HANSKI, 1983; HALFFTER, 1991); whereas in Africa, where carrion is not commonly a dung beetle resource, species are normally restricted to the consumption of herbivore and omnivore dung (CAMBEFORT, 1991a; HANSKI & CAMBEFORT, 1991). In the African continent, the presence of many large carnivores, coupled with carrion birds (vultures), leave little carrion available for beetles. The situation is the reverse in South America. Furthermore, competition between beetles and flies for carrion is higher in Africa than in America (Lumaret, pers. comm.). The fact that the composition and volatile substances of decomposing carrion are more like those of omnivore than herbivore dung (HANSKI, 1987), coupled with the relative numerical scarcity of herbivore and omnivore mammals in Asian and American tropical forests, has given rise, according to some authors (HALFFTER & MATTHEWS, 1966; HANSKI & CAMBEFORT, 1991; HALFFTER, 1991), to necrophagous trophism.

Similarly, dung beetle species in North America are attracted to all kinds of carnivore, herbivore and omnivore dung. The communities inhabiting different types of faeces can be dissimilar and frequently dung beetle species are spatially restricted by faeces availability (GORDON, 1983). Some communities make use of only such herbivore dung as that of rodents (ANDUAGA & HALFFTER, 1991). More than 40% of Western United States species are linked with rodents or turtles (GORDON, 1983). Omnivore dung has been found to be most coprophagan-attracting in North America, while that of herbivores and carnivores attracts a similar number of dung beetles (STEWART, 1967; FINCHER et al., 1970).

Feeding patterns of the dung beetle communities inhabiting Palaearctic temperate biomes seem to be quite different. The Doñana experiment suggests two principal dung groups depending on their faunal composition: herbivore and hu-

man faeces on the one hand; and the carnivore and wild omnivores on the other hand, characterized by a poor attractiveness. Palaearctic dung beetle fauna are not commonly found in carnivore or wild omnivore faeces, and those so found always also occur in herbivore dung (MYSTERUD & WIGER, 1976; CARPANETO & FABBRI, 1983; HANCOX, 1991; HALFFTER & MATTHEWS, 1966). European dung beetles only sporadically, and never exclusively, consume carrion (VEIGA, 1985; LOBO et al., 1992) but only as adult food. In this case, carrion would represent a nitrogen-rich resource of which the mobile adults may take advantage (HANSKI & CAMBEFORT, 1991). However, if the cattle dung chemical composition changes, with more amino-acids, dung beetles are more numerously attracted and dung is attractive for a longer period (LUMARET et al., 1993).

Doñana data indicate that: i) cow and human dung are consumed by most of species represented by their largest abundances and biomass; ii) horse and fallow deer communities are similar to cow and human dung communities, but the species abundance relationship in horse droppings is uneven due the dominant contribution of *O. similis*, *O. opacicollis* and *O. maki* populations; iii) fallow deer communities present very even species abundance relationship; iv) much lesser use is made of dung of other herbivores.

Human dung, exerting the greatest coprophagous attraction in the tropics (PECK & FORSYTH, 1982; HOWDEN & NEALIS, 1975; HALFFTER et al., 1992), seems to be as coprophagous-attracting as herbivore dung in temperate biomes (RAINIO, 1966; FINCHER et al., 1970), and thus, is the only omnivore dung to play such a role there.

Significant variation of dung beetle community with herbivore food type in northern and temperate Europe is not discernible in published data (LANDIN, 1961; RAINIO, 1966; LOBO, 1985; CARPANETO & PIATELLA, 1986; KIRK & RIDSDILL-SMITH, 1986; LUMARET & KIRK, 1991). Only some singular species are sapro-coprophagous (PALESTRINI & ZUNINO, 1985), or are linked to a particular type

of dung, such as rabbit (MARTÍN-PIERA, 1983; ÁVILA et al., 1988; SÁNCHEZ-PIÑERO & ÁVILA, 1991; LUMARET & IBORRA, in press).

Interesting accounts of faunal changes in pastureland, related with livestock changes, have been published. Replacement of sheep with cattle brings with it a more hydrated, abundant and less ephemeral resource. Subsequent qualitative variation in dung beetle community composition has not been observed, but increased total dung beetle biomass and abundance has been, along with alterations in the relative frequency of species (LUMARET et al., 1992). According to other comparisons of faunal composition in the two types of dung (KESSLER et al., 1974; HANSKI & KUUSELA, 1983), communities have been found to be similar, though poorer and with uneven species abundance relationship in sheep dung. Ecologically, the drier and more ephemeral resource provides for fewer opportunities or niche dimensions, thus limiting the number of coexisting species. Therefore, the data suggest that species coexistence is much more dependent on the availability of an adequate dung-type variety than dung-choice. When different kinds of excrements coexist in the same area, it is reasonable to suppose that opportunities for most species increase.

Other studies have indicated that preference for precisely one type of herbivore dung may depend on species size and trophic-reproductive behaviour, or may be influenced by: the relation between the dung water content and the climate; manageability and consistency; or the seasonal availability of dung (GOLJAN, 1953; LANDIN, 1961; RAINIO, 1966; LOBO, 1985).

The individuals of species (except one) captured for the present study were not randomly distributed among the six principal dung bait types, thus demonstrating trophic preference. More than 50% of *A. ictericus*, *A. lineolatus* Illiger and *A. erraticus* were found in cow dung; *S. cicatricosus* (Lucas), *T. momus* and *A. merdarius* in human dung; *Euoniticellus fulvus* (Goeze) in fallow deer droppings (belonging to the 18

species each accounting for more than 5% of total individuals, table 1). More than 25% of the individual total of these 18 species were found in cow, human, horse and fallow deer dung alone, along with the greatest number of wide trophic niche breadth species. Sixteen of these 18 species were found in at least five of the six most attracting dungs (cow, horse, fallow deer, wild boar, deer and human). As previously mentioned abundance and trophic niche breadth are related in such a way that large population species are also broad trophic spectrum.

In the temperate latitudes of Palaearctic Region, species are not trophically segregated, generally making use of both herbivore and human dung, while still preferring some particular type. Our data indicate that the most coprophage attracting faeces are those with greatest richness, abundance and biomass, exerting equal attraction on small population species. For this reason, populations were larger in group A faeces for those species captured in significantly unequal numbers in groups A and B. No more than three individuals, of species exclusive to group B were captured. Put another way, less rich herbivore dung fauna is an impoverished fauna of the more potent coprophagan attracting faeces; which means that there is no fauna exclusive to wild herbivore faces, colonized by domestic mammal and human dung fauna.

Habitat, body size and trophic preferences

The fauna attracted to different kinds of faeces is highly representative of the Doñana National Park, estimated species populations being similar. Generally speaking, species segregation is more a function of differences of habitat than in trophic resource (greater mean niche breadth), so the lack of correlation between trophic and habitat niche breadth should not surprise. The ability to survive in a variety of environments is unrelated to trophic niche breadth. Habitat distribution in Doñana varies from Scarabaeidae to Aphodiidae (Lobo et al., in press) and can be a function of variables other than food source; for example soil texture, tolerance to waterlogging and waterholding soil capacities (Osberg et al., 1994), and vegetative cover (Doube, 1983; Lumaret & Kirk, 1987; Baz, 1988; Galante et al., 1991, 1995). However, choice of a particular type of dung could be conditioned by the habitat preference of its vertebrate source.

Species body size or average weight is unrelated to degree of attraction to faeces types. As seen earlier, polyphagy in species making use of herbivore faeces is normal, so it is not surprising that numbers of both species and individuals increase considerably with increased trophic niche breadth (table 3). Nevertheless, biomass seems to be more evenly distributed among the different trophic categories (generalists and specialists), due to the contribution of the few large body size, stenophagan species. Of the three narrow trophic niche, abundant population species, two are large body size, the ball-roller *S. cicatricosus* and the ball-carrier *T. momus*. These species are captured most often in human dung, perhaps attracted by its high nitrogen content. According to Hanski & Cambefort (1991), ball-rollers compensate food quantity restrictions imposed by transportion over distances from source by generally choosing nutrient-rich omnivore dung.

Trophic generalists and effect of human colonization

Dung beetle community resource partitioning in the Palaearctic Region is not shown by available data to be greatly affected by trophic selection. Preferences that do exist can vary in time and space, depending on dung environment interactions. Unlike the cases of tropical regions and North America, carnivore and non-human omnivore dung attract dung

beetles only slightly, or not at all, and wild herbivore dung fauna seems to be a sub-group of communities that make use of human and domestic mammal dung. Everything suggests, therefore, an undifferentiated attraction towards the effluents and the volatile components of the different types of herbivore faeces. Why are the temperate biomes of the Palaearctic Region different? Why is polyphagy common in herbivore dung species? Why are coprophagan not attracted to carrion or carnivore and omnivore dung?

Man's presence in the Palaearctic Region over so many years may have made dung beetle community structure less sensitive to the trophic dimension. The most widely held view is that domestication of livestock goes back to 10,000-8,000 years BP (Loftus et al., 1994). Furthermore, major changes in European forests (from forest to predominantly open cultivated lands), started as early as 10,000-8,000 years ago in the Mediterranean area and about 5,000 years ago in Western and Central Europe (Mönkkönen & Welsh, 1994 and references therein). Old World mammal populations would thus have been modified throughout the Neolithic period by human activity, especially livestock herding, possibly leading to drastic reduction, or even extinction, of specialized dung beetles, as well as major dietary restrictions in the truly trophic generalist species (carnivore, wild omnivore and herbivore feeding dung) as a response to resource scarcity. Potentially, more herbivore-polyphagous species would have prospered, and possibly extended their geographic range. If, as in other continents, trophic specialist and/or truly generalist Palaearctic dung beetle fauna existed, then today's communities would have been structured over time, by human activity, so much so that in American and Australian regions, less affected until recently by human activity, it has been necessary to import dung beetles to degrade domestic livestock faeces. In USA, grazing mammals were first introduced about 200-300 years ago (Fincher, 1981), coinciding with the large-scale for-est destruction in the eastern regions of North America (Mönkkönen & Welsh, 1994).

If Palaearctic Region community structure before the Neolithic period was similar to that of other regions today, why are there no carnivore dung beetles? Is this an empty niche? Have specialist species, or true generalists, feeding on herbivore, carnivore and wild omnivore dung, become extinct? Human intervention could have reduced the habitat of these vertebrates, but where it still exists, there should be associated dung beetle fauna. Recent historical changes in community structure, due to human impact, would not completely account for the lack of these specialist and truly generalist species. These changes should have occurred in pre-Neolithic times. In other words, could these singular dung beetle fauna date from pre-human colonization of the Palaearctic temperate regions?

It has recently been argued that taxonomic differences between European and North American avifauna stem from both the geographical configuration (particularly topographical) of the continental land masses and events during the Pleistocene (Mönkkönen & Welsh, 1994). Unlike the Palaearctic Region, orientation of the Nearctic mountain ranges has favoured temperate and tropical biota exchange. These authors point out that birds of the Nearctic Region show a wider life history range, a higher number of specialized species, and a greater between-habitat component of biodiversity. Whereas habitat generalism and colonizing abilities were selected from among western Palaearctic species, which have experienced fragmentation and loss of forest habitats, first naturally and later human-induced many times during the past two million years (Mönkkönen & Welsh, 1994). Could the same causes explain the ecological trophic pattern of coprophagous Scarabaeoidea, in both Palaearctic and Nearctic regions?

On the other hand, Mediterranean ecosystems have been invaded and colonized several times in geological and historical terms by generalist invader species of dif-

ferent biogeographical origin (Di Castri, 1990). Iberian Onthophagini illustrates a good example of coexisting lineages coming from different biogeographical origins (Martín Piera, 1983). In this historical context, it can also been hypothetized that old invader dung beetle communities structured by true generalists feeding on all kind of available faeces and strict specialists, would have been substituted for new invaders better adapted to the opening of the new adaptative zone provided by Artiodactyls dung (Cambefort, 1991b; Scholtz & Chow, 1995), and to the Pleistocene habitat fragmentation (Monkönen & Welsch, 1994).

To test the idea that the lack of specialist and true generalist dung beetle fauna is either the result of pre-Neolithic evolutionary events or Neolithic ecologic changes in the Palaearctic Region, three complementary approachesare suggested; two ecological and one phylogenetic.

1. If human activity has favoured today's frequent and abundant species, through sustained, intense modification of available trophic source type and frequency, dung beetle community structure changes should be observed in areas nearly free of human influence. However, it will not be easy to find a site for testing this hypothesis, because of the lack of truly non-human-transformed ecosystems in the Western Palaearctic Region.

2. If the rich local Palaearctic dung beetle community's null (or nearly null) attraction toward carnivore and wild omnivore dung is the result of singular evolutionary adaptations, rather than a response to resource scarcity, then this trophic behaviour was probably a pre-Neolithic adaptation originated before those vertebrate populations decreased.

3. Establishing trophic adaptation age: Polarizing the polyphagy-stenophagy in the primitive derived sense could be inferred from a reconstruction of the phylogenetic relationships among species, and mapping on to the cladogram one or the other trophic pattern (Brooks & McLennan, 1991). A phylogenetic approach

to the habitat use and diet of major Scarabaeoidea's lineages using this methodology, has been recently proposed by Scholtz & Chown (1995).

Available phylogenetic inferences of Palaearctic coprophagous Scarabaeidae indicate repeated establishment of trophic specializations in several lines: primarily in ancestral groups such as the most primitive Geotrupinae (genera Lethrus, Typhaeus, Thorectes; see Zunino, 1984); secondarily in some ancient Palaearctic radiations of the genus Onthophagus (Scarabaeidae), with few representatives today, such as Parentius, and Palaeonthophagus of the latigena group (Martín Piera & Zunino, 1985).

Thus if the most specialized trophic adaptations are confined to high-rank taxa (genera, subgenera and species groups), Palaearctic Region trophic structuring can be inferred to date, at the latest, from before appearance of the human.

Conclusions

1. In the temperate Palaearctic Region, trophic choice little influences Scarabaeoidea dung beetle community resource partitioning. Species are generally attracted to human and all types of herbivore faeces. Thus, polyphagy restricted to these kinds of excrements is the generalized condition. Species segregation is generally more influenced by habitat than trophic resource.

2. Both large- and small-population species are most attracted to human and domestic mammal faeces. There is no exclusively wild herbivore faeces fauna, but rather an impoverished one, in comparison with that of human and domestic ungulate faeces. Carnivore faeces are hardly colonized at all.

3. The lengthy duration of the effects of the human presence in the Palaearctic Region may explain why coprophagous Scarabaeoidea community structure is nearly independent of trophic choice. However, the human impact alone, historically recent, does not explain the observed ab-

sence of a true polyphagy in the regional coprophagous Scarabaeoidea, extremely poor in communities that colonize carnivore and wild omnivore faeces.

Resumen

Discusión comparada sobre las preferencias tróficas en comunidades de escarabajos coprófagos

Se estudia la relevancia de la dimensión trófica en el reparto de recursos, en una comunidad ibérica de escarabeidos coprófagos en el Parque Nacional de Doñana. Se analizaron nueve clases diferentes de excrementos de vertebrados domésticos y salvajes (tabla 1). Los resultados indicaron que existe una atracción indiferenciada a todo tipo de heces de herbívoros y deyecciones humanas (fig. 1, tabla 2). Sin embargo, aunque la eurifagia en este tipo de heces es la condición generalizada, los excrementos de carnívoros y otros omnívoros, apenas son colonizados (fig. 2). No existe una fauna exclusiva de las deyecciones de herbívoros salvajes. Se trata de una fauna empobrecida respecto a la que coloniza las heces humanas y las de ungulados domésticos (figs. 3-6).

Este patrón difiere del que se conoce en otras regiones biogeográficas. Se argumenta que la antigüedad de la transformación antrópica en la Región Paleártica, puede explicar la escasa importancia de la dimensión trófica en la estructura de estas comunidades. Sin embargo, la intervención humana no acaba de explicar la ausencia de una verdadera polifagia, es decir, la colonización indiscriminada de todo tipo de excrementos.

Se sugieren algunas líneas de investigación alternativas que permitirían evaluar si la actual estructuración de las comunidades coprófagas, respecto al factor recurso, es un evento histórico reciente de origen antrópico o, por el contrario, se trata de un evento preneolítico, cuyas causas habrían de investigarse a escala evolutiva.

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