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A taste for dung: food preferences of dung beetles uncovered

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Abstract

Insects represent the most megadiverse animal group, having evolved a wide range of feeding strategies. Among them, dung beetles stand out for their specialization in exploiting decomposing organic matter, particularly excrements. In the Iberian Peninsula, dung beetles typically feed on various types of dung produced by large herbivorous mammals. However, when different types of dung are available, they tend to show a predilection for the most valuable one. In addition, studies using non-native dungs are lacking. Therefore, the aim of this study was to assess whether an Iberian dung beetle community may be attracted to specific dung types, including those from exotic fauna. Fieldwork was carried out in Mataelpino, a town located in Central Spain (Madrid, Spain). A total of six different dungs were used, from animal species with different feeding strategies and geographic origins: African forest buffalo, Asian elephant, brown bear, goat, fallow deer and wild boar. To determine whether dung beetles exhibit attraction for particular dung types, different statistical analyses were carried out on the data collected from field sampling. The results show that dung beetle species behave mostly as generalists, utilizing all the excrements tested. However, it was observed that there were clear preferences for certain types of excrement, notably elephant dung, which is exotic to the region. Buffalo and wild boar dungs were also highly attractive, whereas goat dung exhibited the lowest attractiveness. In conclusion, Iberian dung beetles display a generalist diet although they may exhibit attraction towards specific excrements, including those of exotic origin.

Introduction

Dung beetles (Scarabaeoidea: Aphodiinae, Scarabaeinae, Geotrupinae) are among the most extensively studied terrestrial arthropods (Giménez-Gómez et al., 2020; Raine & Slade, 2019; Spector, 2006). Possessing all of the characteristics of an ideal focal taxon, they have been widely used in ecological research and biodiversity assessments worldwide (Halffter & Favila, 1993; Raine & Slade, 2019; Spector, 2006). Furthermore, dung beetles provide key ecological functions in both natural and human-modified landscapes, particularly in livestock pastures (Andresen & Feer, 2005; Giménez-Gómez et al., 2020; Hanski & Cambefort, 1991; Nichols et al., 2008; Verdú et al., 2018). These functions include nutrient recycling, soil aeration, parasite and pest fly control and secondary seed dispersal (Andressen, 2002; Nichols et al., 2008; Nichols & Gómez, 2014).

Dung beetles are primarily coprophagous, typically feeding on the faeces of large herbivorous mammals (Scholtz et al., 2009). However, they have also been observed consuming other decomposing organic resources such as rotting fruits, fungi, vertebrate carrion and invertebrate remains (Ebert et al., 2019; Giménez-Gómez et al., 2020; Halffter & Mathews, 1966; Hanski & Cambefort, 1991; Scholtz et al., 2009; Stavert et al., 2014; Verdú et al., 2007; Weithmann et al., 2020). The evolutionary origin of coprophagy remains debated. The prevailing hypothesis proposes that it evolved in association with the diversification of large herbivorous mammals during the Cenozoic (Ahrens et al., 2014; Arillo & Ortuño, 2008), although some authors suggest an earlier origin, with the first dung beetles possibly feeding on dinosaur dung (Chin & Gill, 1996; Gunter et al., 2016; Lopes et al., 2023).

In temperate and cold-temperate regions, coprophagy remains the dominant feeding strategy (Ebert et al., 2019). In such habitats, dung beetle communities rely primarily on the excrements of several species of herbivorous mammals (Hanski & Cambefort, 1991; Raine & Slade, 2019; Simmons & Ridsdill-Smith, 2011). In the Iberian Peninsula, several studies

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have explored potential preferences for different dung types among dung beetles (Galante & Cartagena, 1999; Martín-Piera & Lobo, 1996; Sánchez-Piñero & Ávila, 1991; Verdú, 1998; Verdú & Galante, 2002). However, species that are strictly associated with a single dung type appear to be very rare (Galante & Cartagena, 1999; Sánchez-Piñero & Ávila, 1991; Verdú, 1998; Verdú & Galante, 2002). Furthermore, none of these studies has evaluated dung from non-native mammals. In fact, very few studies globally have assessed beetle responses to exotic dung. For example, Australia's native dung beetle fauna, which co-evolved with marsupials, was unable to process the faeces of introduced European livestock (Matthews, 1971). In contrast, in regions with a historical presence of large herbivores, native dung beetles have successfully adapted to the dung of introduced mammals (Whipple & Hoback, 2012).

In recent decades, numerous studies have focused on the impacts of various factors, such as climate change, habitat fragmentation and anthropogenic disturbances, on dung beetle communities (Cuesta et al., 2021; Cuesta & Lobo, 2019; Dortel et al., 2013; Menéndez et al., 2014; Menéndez & Gutiérrez, 2004). However, the effects of these factors on dung beetle–mammal associations remain poorly understood (Raine et al., 2018). The disappearance or decline of mammal populations may cause a cascading effect on dung beetles, with serious consequences for ecosystem structure and functioning (Colwell et al., 2012; Nichols et al., 2016; Raine et al., 2018). Therefore, understanding the resource use and adaptability of dung beetles is essential, particularly in the context of ongoing environmental conditions (Raine et al., 2018).

In this study, we investigated an Iberian dung beetle community to address the following questions: (1) Do dung beetles exhibit a preference for specific dung types? and (2) Are dung beetles attracted to dung from animal species that are non-native to the study area? The corresponding null hypotheses were: (1) dung beetles show a generalist feeding behaviour and (2) there are no significant differences in attraction to dung from native versus exotic species.

Materials and methods

Study area

The study was conducted in the village of Mataelpino, located in the northwest of the Madrid Autonomous Community (Spain). The sampling area corresponds to a semi-open plot used for livestock grazing, situated on the outskirts of the village (Fig. 1). The plot covers 1.16 hectares at an elevation of 1140 m above sea level, with coordinates 40.73° N, 3.96° W. The climate is continental Mediterranean, characterized by cold and humid winters with frequent frosts, and hot, dry summers with periodic drought (Rivas-Martínez, 1983).

The surrounding landscape is predominantly forested, with woodlands dominated by holm oak (*Quercus rotundifolia* Lam.) and Pyrenean oak (*Quercus pyrenaica* Willd.). Among the shrub layer, the most representative species include brooms, junipers and rockroses. The herbaceous layer is mainly composed of pastures grazed by livestock (Rivas-Martínez & Cantó, 1987). These climatic and vegetational features place the area in the lower Supramediterranean bioclimatic belt (Rivas-Martínez, 1983).

The faunal community is also noteworthy, as the dung from domestic and wild animals constitutes the primary food resource for dung beetles. The area supports high levels of livestock activity, particularly cattle (*Bos taurus* Linnaeus, 1758) and horses (*Equus caballus* Linnaeus, 1758). In addition to these dung types, dung beetles may exploit dung from wild herbivores, such as roe deer [*Capreolus capreolus* (Linnaeus, 1758)], Iberian ibex (*Capra pyrenaica* Schinz, 1838) and European rabbit [*Oryctolagus cuniculus* (Linnaeus, 1758)]. They may also use dung from omnivores such as wild boar (*Sus scrofa* Linnaeus, 1758) and red fox [*Vulpes vulpes* (Linnaeus, 1758)], as well as carnivores like the Iberian wolf (*Canis lupus signatus* Cabrera, 1907) (Viejo, 2013). The presence of these diversity of dung types and grazing practices is representative of many areas of the Iberian Peninsula, particularly in central regions and near mountain zones.

Sampling design

To address the proposed hypotheses, a sampling scheme was designed using pitfall traps baited with faeces from different animal species. A total of six dung types were used: African forest buffalo [*Syncerus caffer nanus* (Boddaert, 1785)], Asian elephant (*Elephas maximus* Linnaeus, 1758), brown bear (*Ursus arctos* Linnaeus, 1758), goat (*Capra hircus* Linnaeus, 1758), fallow deer [*Dama dama* (Linnaeus, 1758)] and wild boar. All excrements were provided by the Madrid Zoo Aquarium on the same day of sampling to ensure their freshness. None of the animals had received recent veterinary treatment.

The selection of excrements was based on a bibliographic review of the physicochemical properties of dung types used in different studies (Abdouli et al., 1992; Abdulyekeen et al., 2016; Alhadhrami & Yousif, 1994; Al-Houty & Al-Musalam, 1997; Barfuss et al., 2011; Brody & Pelton, 1988; Chen et al., 1998; Cu et al., 2015; Dhamodharan et al., 2015; Dierenfeld et al., 2000; Doan et al., 2014; Dougall, 1963; Folin & Wentworth, 1910; Frank et al., 2017; Garg et al., 2005, 2006; Gaur et al., 1984; Grenet et al., 1984; Hansen, 1978; Holter, 2016; Holter & Scholtz, 2007; Howery & Pfister, 1990; Irshad et al., 2013; Kannan et al., 2003; Kheira et al., 2017; Kirchmann & Witter, 1992; Leeming et al., 1996; Leslie & Starkey, 1985; Moe & Wegge, 2008; Moore & Bower, 2001; Ngo et al., 2011; Okoroigwe et al., 2010, 2014; Pan-in & Sukasem, 2017; Pérez-Godínez et al., 2017; Portejoie et al., 2004; Rai & Singh, 2012; Sahito et al., 2014; Schwarm et al., 2009; Shah et al., 2007; Somorin et al., 2017; Steyaert et al., 2012; Vodounnou et al., 2016; Whipple & Hoback, 2012; Williams & Haynes, 1995; Yadav et al., 2011; Yadav & Garg, 2011). A database was compiled containing 15 descriptive variables for 18 dung types (Appendix 1: Table S1). A Gower similarity coefficient (Gower, 1971) was used to compare dung types, followed by cluster analysis using the UPGMA amalgamation rule and a SIMPROF analysis. Analyses were conducted using Primer-E software, version 7.0

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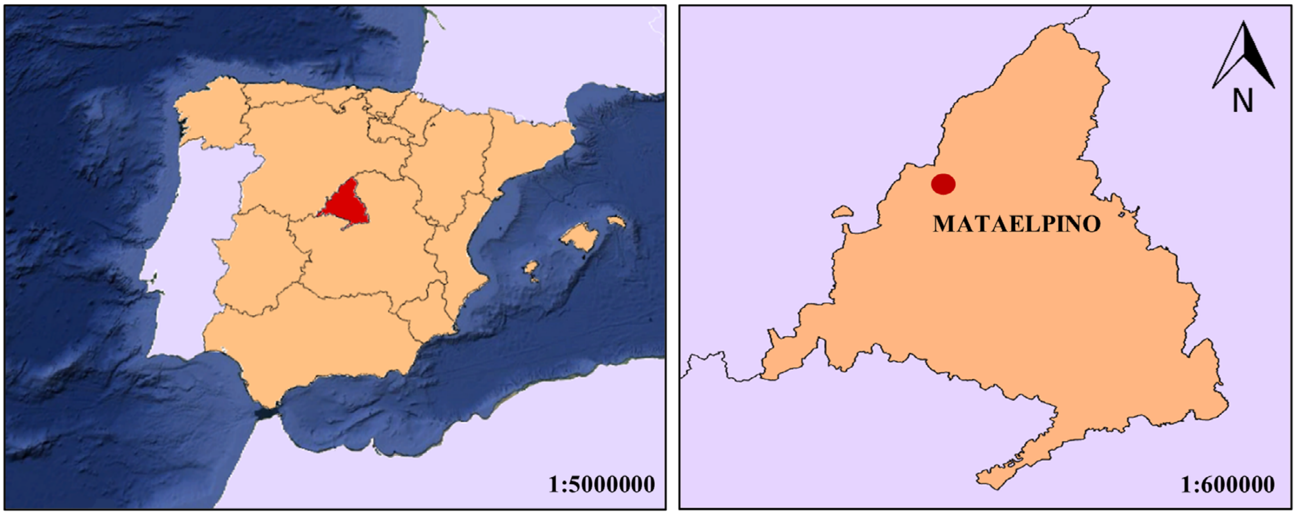

Figure 1 Location maps of the sampling area. The study was conducted in Mataelpino, in the northwest of the Madrid Autonomous Community, central Spain. Coordinates are 40.73° N, 3.96° W. Black lines indicate administrative boundaries.

(Clarke & Gorley, 2015). Representative dung types were selected from each resulting cluster of the dendrogram (Appendix 2: Fig. S1).

To evaluate dung attractiveness, traps were arranged in hexagonal layouts, with each vertex baited with a different dung type. While some studies use inter-trap distances under three metres to simulate natural conditions (Filgueiras et al., 2009; Martínez et al., 2012; Rangel-Acosta et al., 2012), in this case, larger distances were used to avoid overlap between bait odours, both within and between hexagons (Larsen & Forsyth, 2005). Twelve traps arranged in two hexagons were randomly distributed throughout the meadow, with a minimum separation of 50 m between hexagons and at least 10 m between traps within each hexagon (Lobo, 1992a, 1992b; Lobo et al., 1988; Martín-Piera & Lobo, 1996). Two unbaited control traps were also included.

Traps consisted of buried plastic basins filled with a soapy water solution, following the protocol of Lobo et al. (1988) and Veiga et al. (1989). A grid was placed over each basin to hold 250 g of dung (Fig. 2). Sampling was carried out monthly from May 2018 to February 2020. Although the study was initially planned to span 24 months, the final 2 months were interrupted due to the COVID-19 lockdown. Traps remained in the field for 72 h per sampling event (Lobo et al., 1988; Veiga et al., 1989). Collected dung beetles were preserved in 70% ethanol for subsequent identification in the laboratory.

Analytical procedures

Analyses were conducted to determine which dung types were the most attractive to dung beetles. Data from the two monthly traps per dung type were pooled. Analyses were performed for the entire community of coprophagous Scarabaeoidea as well as for each subfamily separately (Aphodiinae, Geotrupinae and Scarabaeinae).

Figure 2 Example of a pitfall trap used in the field. The photograph illustrates a typical pitfall trap deployed under field conditions for sampling dung beetles.

An estimation of species diversity was conducted for each dung type using the method proposed by Chao and Jost (2015), based on the Hill numbers framework (Chao et al., 2021, 2023; Hill, 1973). This approach generates diversity profiles as a continuous function of the parameter q. Specifically, $q = 0$ corresponds to potential species richness, $q = 1$ to the exponential Shannon entropy (i.e. effective number of abundant species), and $q = 2$ to the inverse Simpson index (i.e. effective number of dominant species) (Chao et al., 2014, 2020, 2021, 2023; Chao & Jost, 2015). Sampling completeness was assessed by comparing observed to estimated richness, with values above 70% considered indicative of adequate sampling effort (Jiménez-Valverde & Hortal, 2003). Analyses were performed using the R package SpadeR version 0.1.1 (R Core Team, 2022) and the Diversity function to compute diversity

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estimates (Chao et al., 2016). Thus, diversity profiles, the observed abundance of individuals (Ab) and the species richness obtained (R_0) from the field data, all quantitative variables, were considered as study variables.

Non-parametric tests were used to compare the diversity parameters obtained for each dung type, as not all variables followed a normal distribution. Since the data consisted of dependent samples across sampling dates, a Friedman ANOVA test was applied (Friedman, 1937, 1940), which allows the analysis of three or more repeated measures for ordinal or non-normally distributed data. Subsequently, Wilcoxon signed-rank tests were used for pairwise comparisons (Wilcoxon, 1945), applying Bonferroni corrections to control for Type I error. These analyses allowed us to determine whether dung beetle communities exhibited attraction for a particular type of dung or whether they were homogeneously distributed across the different dung types. All statistical analyses were conducted using STATISTICA 10 (StatSoft Inc., 2011).

In addition, interaction network analyses were used to illustrate and quantify the trophic associations between dung beetles and dung types. Three indices were calculated: linkage density (Bersier et al., 2002), H_2' (a network-level specialization metric; Blüthgen et al., 2006) and WNODF (Weighted Nestedness metric based on Overlap and Decreasing Fill; Almeida-Neto & Ulrich, 2011). Linkage density represents the average number of interactions per species. The H_2' index ranges from 0 (no specialization, with beetle species using dung types in similar proportions) to 1 (maximum specialization, where each beetle species uses a specific dung type exclusively). WNODF values range from 0 to 100, with 100 indicating a perfectly nested network structure. To assess whether the observed network structures differed significantly from random expectations, a null model analysis was conducted. A total of 10 000 randomized networks were generated using the *bipartite* package (Dormann et al., 2008), constraining both the total species abundances and the number of links. Observed values of each index were then compared to the distribution of values from the null models using one-sample *t*-tests (Dormann et al., 2009). These analyses were performed using the SpadeR package version 0.1.1 in R (R Core Team, 2022).

Finally, a comparative analysis was performed to determine which dung type supported the greatest phylogenetic diversity of dung beetles. The method described by Vane-Wright et al. (1991) was followed. Each species was assigned a score based on its position in a consensus phylogeny and its phylogenetic relationships with other species. The phylogenetic diversity associated with each dung type was then calculated as the cumulative sum of the scores of the species present in that dung. If a dung type reached 100%, it indicated that it harboured all the phylogenetic diversity found in the study. If none of the dung types reached 100%, a prioritization scheme was applied by sequentially removing the most diverse dung types and recalculating scores, allowing identification of secondary contributors to overall phylogenetic diversity. The consensus phylogeny was built using information from published phylogenies and taxonomic studies relevant to the recorded species (Cabrero-Sañudo, 2007; Cabrero-Sañudo & Zardoya, 2004; Cunha et al., 2011; Macagno et al., 2011; Martín-Piera, 2001; Martín-Piera & López-Colón, 2000; Pizzo et al., 2006, 2013; Verdú et al., 2004; Villalba et al., 2002).

Results

A total of 59 264 dung beetles belonging to 46 species were collected (Appendix 1: Table S2). These included 24 species and 52 959 individuals from the subfamily Aphodiinae, 18 species and 6216 individuals from Scarabaeinae, and four species and 89 individuals from Geotrupinae. No representatives of the Geotrupinae subfamily were collected in goat dung. When comparing dung types, elephant dung yielded the highest results, followed by buffalo and wild boar dungs. In contrast, bear dung displayed the most heterogeneous values, while goat dung yielded the lowest values (Table 1; Appendix 2: Fig. S2).

Regarding the sampling effort validation, almost all ratios were equal to or higher than 70.00%, with the exception of goat dung (Table 1). However, since its value was close to 70%, it was considered acceptable, and the data were assumed to adequately represent the dung beetle community. Fallow deer and bear dung showed the highest representation values (>90%), followed by buffalo and wild boar dung, with 86.67 and 83.22%, respectively. Elephant and goat dung exhibited the lowest representation values.

Across dung types, the patterns observed in diversity indices closely mirrored those for species richness (Fig. 3). In most cases, elephant dung supported the highest values, followed by buffalo dung. Goat dung consistently yielded the lowest values, while bear and fallow deer dung showed intermediate or low values, particularly in terms of abundance.

When comparing the dung types, no significant differences were found between elephant and buffalo dungs, except for Geotrupinae abundance, which was highest in elephant dung. In contrast, significant differences were observed between these two types and goat or fallow deer dung. Results from wild

Table 1 Results of the diversity estimation method for the different dung types

	q_0	q_1	q_2	Observed richness (R_0)	Abundance (Ab)	R_0/q_0 ratio (%)
Buffalo	45.000	5.263	3.214	39	9265	86.67
Elephant	60.000	4.150	3.147	42	27 547	70.00
Goat	32.120	2.277	1.586	22	1979	68.49
Fallow deer	31.785	2.759	1.878	30	3482	94.38
Wild boar	37.250	3.229	2.187	31	15 086	83.22
Bear	27.000	7.862	5.215	25	1905	92.59

Values shown correspond to potential species richness (q_0), exponential Shannon diversity (q_1) and inverse Simpson diversity (q_2). Also shown are observed abundance (Ab), observed species richness (R_0) and the sampling effort validation as the ratio R_0/q_0. Sampling is considered representative when this ratio value is ≥70.00%.

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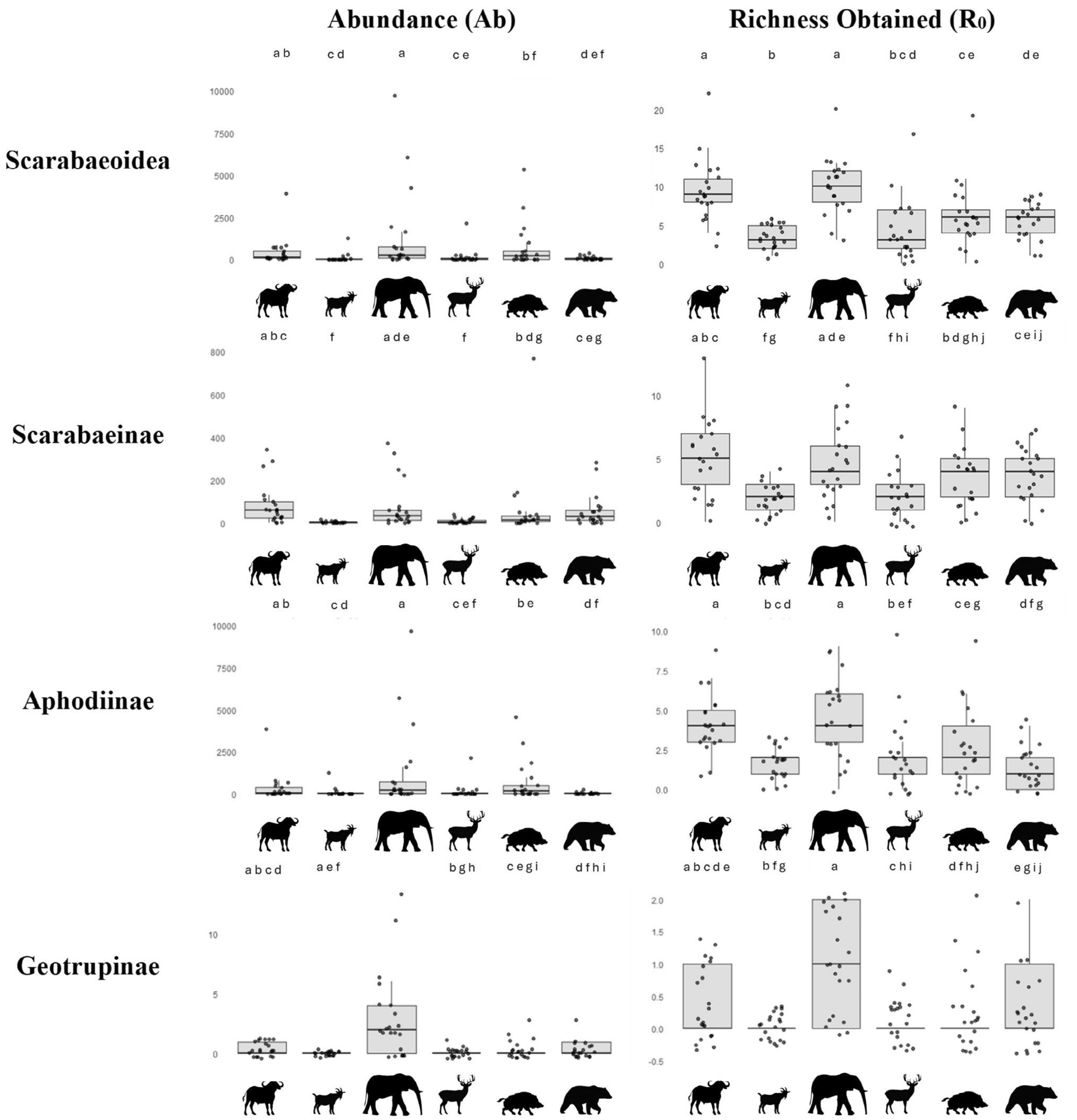

Figure 3 Graphical representation of non-parametric analyses. Results for abundance (Ab) and observed richness (R_0) in the field are shown for all dung beetles combined (coprophagous Scarabaeoidea) and separately for each subfamily (Aphodiinae, Geotrupinae and Scarabaeinae). Each graph identifies the corresponding excrement. Lowercase letters indicate pairs of dung types between which statistically non-significant differences were detected.

boar and bear dung were more heterogeneous; overall, no significant differences were found between them, although they tended to differ from buffalo and elephant dung. Notably, within the Scarabaeinae subfamily, differences among buffalo, elephant, wild boar and bear dung were not significant.

The interaction networks comprised the 46 recorded species (combined and grouped by subfamilies) and the six dung types (Fig. 4). Low H_2' values were recorded across all taxonomic levels, suggesting low specialization. Linkage density was relatively high, especially in the Scarabaeinae community. The

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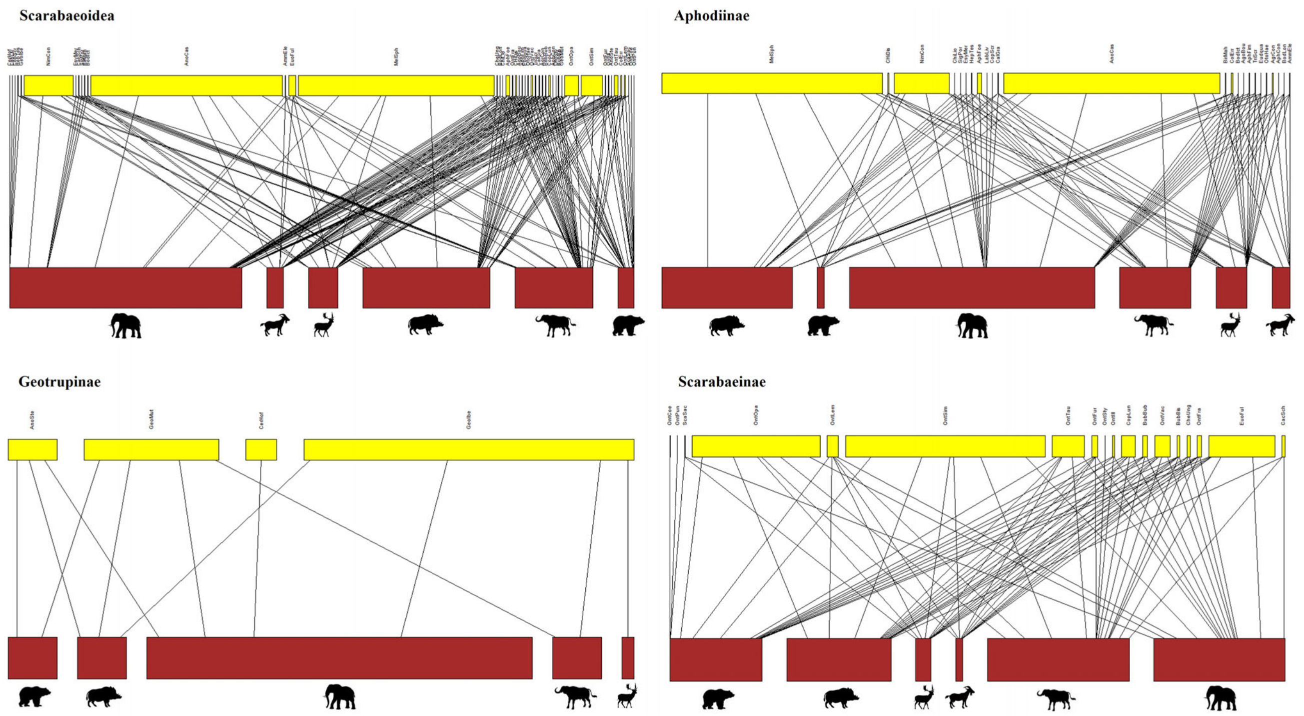

Figure 4 Dung beetle interaction networks. Interaction networks are presented for all dung beetles combined (coprophagous Scarabaeoidea) and separately for each subfamily (Aphodiinae, Geotrupinae and Scarabaeinae). The networks depict interactions between dung beetle species and dung types, based on beetle abundance. Connecting bars represent the links between species and dung types. Upper bars: width proportional to total abundance of each dung beetle species; lower bars: width proportional to the number of occurrences of each species in each dung type. Each graph identifies the corresponding excrement. Species abbreviations are as follows: *Agolius bonvouloiri* (AgoBou); *Agrilinus constans* (AgrCon); *Aphodius conjugatus* (AphCon); *Aphodius fimetarius* (AphFim); *Aphodius foetidus* (AphFoe); *Ammoecius elevatus* (AmmEle); *Anomius castaneus* (AnoCast); *Biralus mahunkaorum* (BirMah); *Bodiloides ictericus* (BodIct); *Calamosternus granarius* (CalGra); *Chilothorax distinctus* (ChiDis); *Chilothorax lineolatus* (ChiLin); *Colobopterus erraticus* (ColErr); *Coprimorphus scrutator* (CopScr); *Esymus merdarius* (EsyMer); *Eudolus quadriguttatus* (EudQua); *Heptaulacus testudinarius* (HepTes); *Labarrus lividus* (LabLiv); *Melinopterus sphacelatus* (MelSph); *Nimbus contaminatus* (NimCon); *Otophorus haemorrhoidalis* (OtoHae); *Sigorus porcus* (SigPor); *Trichonotulus scrofa* (TriScr); *Bubas bison* (BubBis); *Bubas bubalus* (BubBub); *Caccobius schreberi* (CacSch); *Cheironitis ungaricus* (CheUng); *Copris lunaris* (CopLun); *Euoniticellus fulvus* (EuoFul); *Onthophagus coenobita* (OntCoe); *Onthophagus fracticornis* (OntFra); *Onthophagus furcatus* (OntFur); *Onthophagus illyricus* (OntIll); *Onthophagus lemur* (OntLem); *Onthophagus opacicollis* (OntOpa); *Onthophagus punctatus* (OntPun); *Onthophagus similis* (OntSim); *Onthophagus stylocerus* (OntSty); *Onthophagus taurus* (OntTau); *Onthophagus vacca* (OntVac); *Scarabaeus sacer* (ScaSac); *Anoplotrupes stercorosus* (AnoSte); *Geotrupes ibericus* (GeoIbe); *Geotrupes mutator* (GeoMut); *Ceratophyus hoffmannseggi* (CerHof).

Aphodiinae subfamily exhibited the highest WNODF value, suggesting a nested structure. For all subfamilies except for the Geotrupinae, linkage density and H_2' values differed significantly from null model expectations, indicating non-random patterns. In contrast, the WNODF index did not differ significantly from random expectations (Appendix 1; Table S3).

The comparative analysis showed that elephant dung consistently supported the highest species diversity, ranking first in all cases (Table 2; Appendix 2; Figs. S3 and S4). All Geotrupinae species (100%) were recorded in elephant dung. Within Aphodiinae, 96.94% of species were present in elephant dung, with only *Aphodius conjugatus* Mulsant, 1842, absent – this species was exclusive to buffalo dung (3.06%). According to the Vane-Wright method, elephant dung contained the greatest diversity and could be best complemented by buffalo dung to represent the full set of taxa. In Scarabaeinae, approximately 90% of species found were found in elephant dung. Only *Onthophagus punctatus* (Illiger, 1803) and *O. coenobita* (Herbst, 1783) were absent (exclusive to bear dung; 8.39%), along with *O. stylocerus* Graëlls, 1851, found only in buffalo dung (3.23%). Thus, elephant dung would have the greatest diversity and then bear and buffalo dung ensure a complete taxonomic representation.

Discussion

The results of this study confirm that dung beetles are attracted to different types of dung. A large number of species were collected across all dung types, demonstrating considerable trophic plasticity. However, some dung types were more effective at attracting higher abundance and richness of dung beetles. Moreover, beetles did not appear to face significant limitations

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Table 2 Results of the comparative analysis based on the Vane-Wright et al. method (1991)

	Buffalo (%)	Elephant (%)	Goat	Fallow deer	Wild boar	Bear
Scarabaeinae	78.69	88.38%	60.15%	70.91%	75.46%	83.00%
	3.23	—	—	—	—	8.39%
Aphodiinae	89.80	96.94%	50.00%	71.43%	52.04%	30.61%
	3.06	—	—	—	—	—
Geotrupinae	30.77	100%	0%	15.38%	53.85%	38.46%

Each species was assigned a diversity score according to its phylogenetic distinctiveness. The dung type(s) with the highest cumulative scores are prioritized. Percentages indicate priority ranking, with 100% corresponding to the dung type housing the greatest diversity. Significant dung types are marked in red.

in colonizing dung from non-native animals, underscoring their adaptability to novel resources.

Dung beetle communities associated with each dung type were relatively homogeneous, sharing a high percentage of species. In fact, a certain degree of community nesting was observed. Numerous linkages between dung types were detected, along with very low H_2' index values. These findings point to opportunistic and generalist-feeding habits (Hanski & Cambefort, 1991; Raine & Slade, 2019; Simmons & Ridsdill-Smith, 2011), a pattern commonly observed in dung beetles from temperate Palearctic regions. Cases of species specialized in a single dung type are extremely rare in Mediterranean ecosystems (Galante & Cartagena, 1999; Lumaret & Iborra, 1996; Sánchez-Piñero & Ávila, 1991; Verdú, 1998; Verdú & Galante, 2002, 2004). Given the ephemeral and patchy nature of dung, extreme specialization in dung beetles is considered highly unlikely (Finn & Giller, 2002; Halffter & Matthews, 1966; Hanski & Cambefort, 1991; Lobo, 1992a). In our study, only a few species were found exclusively in one dung type, but they were represented by very few individuals, in some cases just one. Furthermore, previous studies report that these species also occur in other dung types (Barbero et al., 1999; Martín-Piera & López-Colón, 2000; Sánchez-Piñero & Ávila, 1991).

Despite the general tendencies observed, some dung types were clearly more attractive, supporting the hypothesis of *choosy generalism*, proposed for dung beetles (Dormont et al., 2004, 2007; Frank, Brückner, et al., 2018; Urrutia et al., 2022). According to this hypothesis, generalist species can select the most valuable resource when multiple options are available. Volatile organic compounds (VOCs) are thought to play a central role in this selection process (Dormont et al., 2004, 2007, 2010; Frank, Brückner, et al., 2018; Frank, Krell, et al., 2018; Wurmitzer et al., 2017). Each dung type has a specific VOC profile, including both shared and unique compounds (Dormont et al., 2007, 2010), which may explain the differences in attractiveness observed in our study. Elephant dung, for instance, attracted the highest number of individuals and the greatest species diversity. These results are consistent with previous findings (Hewavithana et al., 2016; Vinod & Sabu, 2007), which identified elephant dung as especially attractive, possibly due to its distinctive VOC bouquet. Buffalo dung was also highly attractive, yielding results similar to those for elephant dung (Hewavithana et al., 2016), although overall beetle abundance was lower. As a close analogue to cattle dung – a commonly used resource in numerous studies – buffalo dung performs similarly and may benefit from regional familiarity, as local dung beetle communities are well adapted to livestock dung (Errouissi et al., 2004; Galante & Cartagena, 1999; Martín-Piera & Lobo, 1996; Tiberg & Floate, 2011). Wild boar dung also proved effective, supporting a diverse and abundant beetle community and was the second most attractive dung type in terms of total abundance. Its VOC composition resembles that of cattle dung (Frank, Brückner, et al., 2018), which may explain its attractiveness in this study.

In contrast, fallow deer and bear dung were among the least attractive types. This agrees with previous studies (Dormont et al., 2007; Frank, Krell, et al., 2018; Hewavithana et al., 2016; Martín-Piera & Lobo, 1996). Goat dung was the least attractive dung type in this study. Although goat or sheep dung can be effective in cooler, more humid environments (Dormont et al., 2007, 2010; Errouissi et al., 2004; Finn & Giller, 2002), its rapid desiccation under Mediterranean conditions likely reduces its attractiveness.

Although olfactory cues appear central to dung selection, other physical features may influence dung attractiveness. For instance, the shape and texture of the dung can either extend or reduce its attracting power. Pellet-like, fibrous dung (e.g. goat or fallow deer) dries rapidly, losing attractiveness quickly (Errouissi et al., 2004). In contrast, dung types with a dungpat structure (e.g. cattle or buffalo) form a surface crust that retains moisture, preserving attractiveness for longer periods (Lumaret & Kirk, 1987). Although dung amount was standardized in this study, larger dung volumes generally enhance attractiveness (Frank et al., 2017).

Dung nutritional composition might also play a role, given the dietary differences among source animals. Carnivore dung is richer in essential nutrients such as amino acids and sterols, which are essential for the proper development of insects (Frank et al., 2017) but may contain harmful bacteria detectable by dung beetles. Omnivore dung presents intermediate nutritional values, while herbivore dung is typically less nutritious. Nevertheless, dung beetles can extract necessary nutrients from various dung types, as shown by Frank et al. (2017), suggesting that nutritional quality has limited influence on dung choice.

While trophic preferences of dung beetles have been extensively studied in the Iberian Peninsula, this is the first study to include dung from exotic animals. In line with other international studies (Gittings & Giller, 1998; Whipple &

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Hoback, 2012), our results show that the origin of dung (native or exotic) does not strongly affect beetle attraction. For example, elephant dung – non-native to the study area – attracted a highly diverse assemblage, including all recorded Geotrupinae species, nearly all Aphodiinae, and over 85% of the Scarabaeinae. Thus, other factors, such as VOC composition, likely drive dung beetle preferences.

Finally, it is important to note that dung attractiveness is not determined solely by dung-intrinsic features (Dormont et al., 2004, 2007, 2010; Frank et al., 2017; Frank, Brückner, et al., 2018; Holter, 2016; Stavert et al., 2014), but also by extrinsic factors such as habitat type (Barbero et al., 1999) or beetle-specific biological requirements (Dormont et al., 2004). Consequently, dung beetle attraction results from a combination of historical, geographical or ecological factors, which should be considered in future studies (Barbero et al., 1999). Furthermore, global environmental changes, such as the decline of large herbivores, may adversely affect dung beetle communities and the ecosystem functions they provide (Raine et al., 2018). Thus, a deeper understanding of dung beetles' feeding ecology and trophic plasticity is crucial for anticipating potential ecological shifts.

It is not possible to determine with certainty whether the spatial arrangement of the dung types in our experimental setup influenced the results. To our knowledge, no general study has yet established the effective sampling area (ESA) for dung beetles, which would define the optimal spacing to avoid overlap in the attractant effects of baits. Some authors have proposed minimum distances to reduce trap interference based on specific contexts. Larsen and Forsyth (2005) suggested a standardized inter-trap distance of 50 m, based on experiments with a single dung beetle species in a semi-deciduous tropical forest. More recently, da Silva and Medina (2015) proposed increasing this distance to 100 m, based on results obtained in the Brazilian Atlantic Forest. However, the general applicability of these distances remains uncertain, as attraction ranges are likely to vary depending on the species, habitat and environmental conditions. In our study, traps within each sampling unit (hexagon) were spaced 10 m apart, and at least 20 m separated traps belonging to different hexagons. Given the absence of conclusive data and the logistical constraints of deploying a large number of baited traps, our setup represents a conservative compromise aimed at reducing potential overlap while maintaining spatial replication.

In conclusion, this study confirms the trophic flexibility of dung beetles, supporting the idea that they are generalist species with differential preferences. The results highlight the importance of using a wide variety of dung types, both native and exotic, to capture the full spectrum of community-level responses. Our findings also emphasize that functional redundancy in dung beetles is only apparent and that changes in the composition or availability of dung types may have important consequences for ecosystem processes mediated by these insects.

Conclusions

Our results show consistent differences in dung beetle assemblages among dung types, both in species composition and relative abundance. These patterns suggest that dung beetles exhibit plasticity in their trophic responses, leading to apparent preferences when simultaneously exposed to different types of dung. While our findings do not allow us to infer true selection or adaptive processes in the evolutionary sense, they do reveal a non-random use of dung types by various species. This variation in dung use may have important implications for the role of dung beetles in ecosystem functioning, particularly in heterogeneous landscapes where multiple types of dung are available.

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Author contributions

Sandra Grzechnik and Francisco José Cabrero Sañudo conceived the study and designed the methodology. Both authors conducted fieldwork, analysed the data and led the writing of the manuscript. All authors contributed critically to manuscript drafts and approved the final version for publication.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Summary table of the literature review.

Table S2. List of the 46 dung beetle species recorded in Mataelpino, organized by subfamilies.

Table S3. Results of the interaction network analyses.

Figure S1. Dendrogram resulting from hierarchical clustering based on the Gower similarity coefficient.

Figure S2. Diversity profiles based on Hill numbers.

Figure S3. Graphical representation of dung selection by dung beetle species.

Figure S4. Phylogenetics relationships among the dung beetle species recorded in the study area, with subfamilies Aphodiinae, Scarabaeinae, and Geotrupinae differentiated.

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