Comparison of Spatial Distribution Patterns of Dung-Feeding Scarabs (Coleoptera: Scarabaeidae, Geotrupidae) in Wooded and Open Pastureland in the Mediterranean "Dehesa" Area of the Iberian Peninsula

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ABSTRACT The seasonal and spatial distributions of dung-feeding scarabs in an open pastureland and in wooded (holm oak) pastureland in a typical Mediterranean area of the western part of the Iberian Peninsula (Salamanca) were compared. Six pitfall traps baited with bovine dung were placed in each habitat according to a model by J. P. Lumaret. Only beetles in the families Scarabaeidae and Geotrupidae were studied because they are the most important agents in the elimination of cattle dung from the soil surface. Weekly trapping for 1 yr produced 6,909 specimens. Of the 18 species found, the largest beetles and biomass were concentrated mainly in the wooded habitat, especially in the summer. This constitutes a problem for dung removal because large amounts of dung remain in open pasturelands, possibly resulting in the impoverishment of such areas.

KEY WORDS Insecta, dung beetles, Scarabaeidae, Geotrupidae

LAND USED FOR GRAZING constitutes a characteristic ecosystem in which detritivore food chains predominate. In such chains, much of the primary net productivity is not used by the herbivores that live in the area, but by numerous ground-dwelling organisms. As indicated by Desiere (1983), more than half the food consumed by the herbivores is returned to the ground in the form of unassimilated material; i.e., the dung. Because of its abundance in organic material and its peculiar microclimatic conditions, cattle dung is an ideal medium for the establishment of a specific, rich, and varied kind of biocenosis (Finne & Desiere 1971, Graef & Desiere 1984) involving the processes of decomposition and elimination of feces.

Among dung-feeding species, the scarabs (Coleoptera: Scarabaeoidea) play a very important role in the rapid-recycling processes of dung, as indicated by Fincher et al. (1981). They are also of great importance in the physical–chemical alteration processes of the soil, especially the larger species. The activity of dung-feeding scarabs implies a series of indirect benefits for both livestock and pasture (Bornemissza & Williams 1970, Castle & Macdaid 1972, Hughes et al. 1978, Fincher 1981, Rougon & Rougon 1981, Rougon et al. 1988).

In the Mediterranean Region, the decomposition of organic materials and the recycling of bioelements are characterized by their slowness (Lumaret 1983). This is a limiting factor in the productivity of ecosystems. An indispensable condition for the correct functioning of all pasture ecosystems is that the dung be rapidly utilized and transformed. If this does not occur, dung deposited on the soil can eventually cause serious damage because it deteriorates the pastureland by preventing plant growth (Bastiman 1970, Waterhouse 1974, Lumaret 1986). As a secondary effect, this situation leads to an increase in the population of dung-breeding flies and the loss of nitrogen by volatilization, which then cannot be incorporated into the soil. Communities rich in dung-feeding scarabs that are able to degrade cattle feces efficiently are of great economic importance. The province of Salamanca is one of the regions of Spain with a large number of free-roaming cattle all year round. This, together with its long tradition in cattle breeding, makes the area ideal for studies on the dynamics of dung-feeding scarab communities (Galante 1978, 1979, 1981).

The purpose of this study was to gain insight into the yearly spatial distribution of the different species of dung-eating scarabs in Mediterranean holm oak areas. The vegetational ground cover seems to be an important factor in the local distribution of coprophagous fauna (Halffter & Matthews 1966, Howden & Nealis 1975, Halftter & Edmonds 1982, etc.). Accordingly, our aim was to discover the effect of the alteration of the environment due to tree felling and the transformation of wooded areas into open pastureland on the communities of certain dung-feeding scarabs.

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Table 1. Species phenology and average biomass of individual beetles for each species and percentage of the total biomass for each species represented.

Species[a]	Phenology[b]								Biomass	
	Spring		Summer		Autumn		Winter		Mg dry wt insect	
	W	O	W	O	W	O	W	O	$\bar{x} \pm$ SD (n = 20)	%
Gymnopleurus flagellatus	—	—	—	6	—	—	—	—	46.2 ± 17.4	0.064
1 *Copris lunaris*	72	21	418	13	12	1	—	—	286 ± 50	35.84
2 *Copris hispanus*	11	15	32	—	15	4	—	—	336.6 ± 88.9	6.05
Chironitis hungaricus	—	—	—	4	—	—	—	—	34.3 ± 8.25	0.032
3 *Onitis belial*	—	—	1	5	—	—	—	—	231.5 ± 108	0.324
4 *Bubas bubalus*	101	141	402	162	94	35	1	1	173.2 ± 31.2	37.87
5 *Euonitticellus fulvus*	—	8	39	71	2	6	—	—	5.93 ± 1.5	0.174
6 *Caccobius schreberi*	—	26	38	192	—	—	—	—	5.52 ± 1.12	0.329
7 *Onthophagus taurus*	—	11	6	24	—	1	—	—	14.6 ± 5.2	0.143
8 *Onthophagus punctatus*	—	1	1	—	1	—	—	—	8.6 ± 2.46	0.006
9 *Onthophagus furcatus*	—	4	25	3	—	—	—	—	2.83 ± 1.06	0.021
10 *Onthophagus ruficapillus*	3	480	30	172	—	—	—	—	4.76 ± 0.8	0.76
11 *Onthophagus coenobita*	5	—	—	—	—	—	—	—	17.5 ± 4.32	0.02
12 *Onthophagus similis*	477	1,050	1,003	294	289	562	5	86	8.25 ± 2.17	7.25
13 *Onthophagus vacca*	9	52	51	73	—	5	—	—	25 ± 5.9	1.108
14 *Typhaeus typhoeus*	12	2	—	—	24	—	11	—	110.9 ± 44.2	1.268
15 *Geotrupes mutator*	22	2	11	5	54	7	14	1	212.3 ± 80	5.747
16 *Geotrupes ibericus*	2	1	29	1	35	3	—	1	177.4 ± 48	2.98

[a] The number that precedes each species corresponds to the number used in the statistical processing and appears in the HJ-Biplot graphs.
[b] W, wooded habitat; O, pasture.

Materials and Methods

The study was conducted on the Castro Enriquez experimental cattle farm, in Aldehuela de la Bóveda, Salamanca, Spain. This farm has 400 ha of pasture dedicated to year-round grazing for cattle. The usual number of cattle on pasture is ≈200 adults with varying numbers of yearlings and calves. During the year, the cattle are herded from one place to another within this area.

Rainfall and daily temperatures were monitored at a meteorological station (Barbadillos, Salamanca) 15 km from the study site.

The climax vegetation is the Mediterranean holm oak, with a predominance of *Quercus rotundifolia* Lam. The farm consists of a clear-felled savanna-like woodland ("dehesa"), with little underbrush, that serves as grazing land. These zones alternate with areas transformed by human activity into open pastureland with no trees or shrubs.

Two plots were selected (10 by 10 m): one wooded with no underbrush and the other 150 m away in open pasture. Both plots were fenced to keep cattle out. Sampling was done by using pit-fall traps according to Lumaret (1979). The bait was 56 cm^3 of fresh bovine feces for each trap (38 ± 3 g dry weight). As a preserving fluid, 200 ml of 50% ethylene glycol was used. This type of trap has the advantage of permitting optimum diffusion of the volatile elements of the feces at ground level. Two rows of three traps each were placed in each plot, for a total of six traps in the wooded area and six traps in the open area. The distance between each row and trap was 3 m. The feces used as bait and the preserving fluid with the fauna that it contained were collected every 7 d for 1 yr (December 1985–November 1986). After collection, fresh feces and preserving fluid were replaced. Thus, the entire sequence of the annual surface activity of the coprophagous fauna was followed. Only beetles of the families Scarabaeidae and Geotrupidae were analyzed. The species in these families are very important agents in decomposing cattle dung because of their biomass (Table 1) and their feeding and breeding habits (Halffter & Edmonds 1982).

In addition, an attempt was made to distinguish and characterize the two habitats (holm oak wooded area and open pastureland) based on the density or abundance of each species of dung-eating scarabs.

The statistical technique used was the HJ-Biplot multidimensional data classification technique (Galindo-Villardón 1986), which is a variant of the biplot graphic display proposed by Gabriel (1971). This technique makes it possible to plot the rows and columns of the data matrix as points on a low dimension vector space. It has been shown theoretically (Galindo-Villardón 1986) that the quality of plotting both for populations and for variables is superior to that achieved with similar techniques. Also, the discriminatory power of this statistical technique has been demonstrated in other biological studies (Perez-Mellado & Galindo-Villardón 1986, Castrillo et al. 1986). To make the equilibrium points of the two clouds (variables and populations) coincide, the data were subjected to a double centering. The proximity of the points that represent the scarab groups of study is interpreted in terms of similarity, and the proximity of these points to those representing the species is interpreted in terms of preponderance.

The approximation to a low range was made according to Golub & Reinsch (1970) and the computer analysis was carried out using the RSDM package (Galindo et al. 1990).

The works of Zunino (1972), Baraud (1977), Martín-Piera (1983, 1984), Martín-Piera & Zunino (1986), and Paulian & Baraud (1987) have basically been followed in the determination and systematics.

The biomass per species was obtained by calculating the mean weight of 20 specimens (10 ♂♂ and 10 ♀♀). These were dehydrated at 60°C for 72 h and were weighed subsequently on a precision balance.

Results

The ombrothermic diagram (Fig. 1) indicates a period of severe drought with high temperatures corresponding to the months of June (in part), July, August, and September (in part).

A total of 6,909 specimens were captured; of these, 18 species (15 Scarabaeidae and 3 Geotrupidae) were found (Table 1). A comparative test was applied to the six traps in each habitat and no significant differences were obtained.

Fig. 2 and 3, drawn according to Luis-Calabuig & Purroy (1980), show the annual evolution of the different species of dung-feeding scarabs in each habitat. In most cases, the same species were found in the wooded and open habitats but the number of specimens captured and when they were most active were different. They were thus classified into eight groups according to season–community: 1. Spring–Wooded pastureland; 2. Spring–Open pastureland; 3. Summer–Wooded pastureland; 4. Summer–Open pastureland; 5. Fall–Wooded pastureland; 6. Fall–Open pastureland; 7. Winter–Wooded pastureland; and 8. Winter–Open pastureland.

Spring was considered to be March, April, and May; summer was June, July, and August; fall was September, October, and November; and winter was December, January, and February.

The initial frequency distribution is shown in Table 1. Only six specimens of *Gymnopleurus flagellatus* F. 1787 and four specimens of *Chironitis hungaricus* (Herbst 1789) were collected in open pastureland in the summer. In the winter period, only five species were found, each with very few specimens. Winter activity was similar in both environments. Accordingly, only the first six groups and the first 16 species are involved in the statistical study.

Fig. 4 shows the HJ-Biplot of the data table (Table 1). Because this is a technique involving the simultaneous representation of multidimensional data, the two hyperclouds appear as projections on the principal plane. The first principal axis absorbs 82% of the inertia and the weight of the plane is 89%. The goodness of fit for both the groups under study and the species is 98.8%.

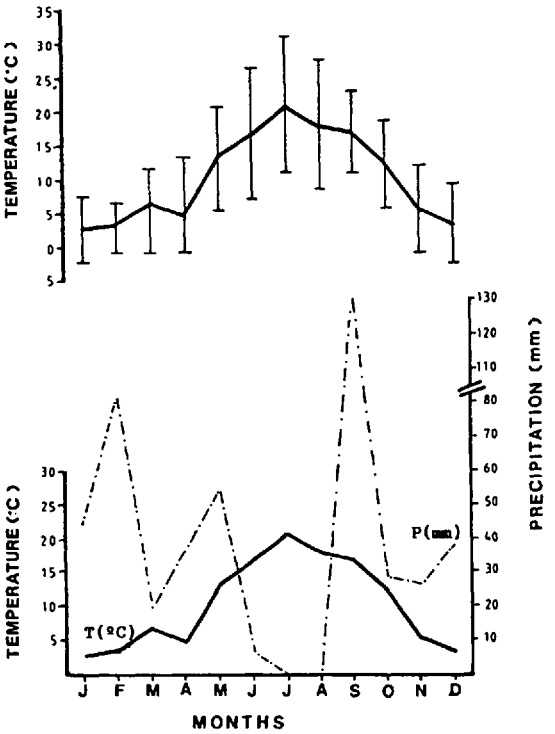

Fig. 1. The upper graphs show the monthly maximum and minimum air temperatures as well as the average annual temperature in Muñovela, Barbadillo, Salamanca (15 km NW of the study area). The lower graph shows the ombrothermic diagram of Bagnouls and Gaussen in the study area. Data provided by the National Institute of Meteorology, Spain.

The first Eigenvalue is 63.61 and the second, 19.26. Both are perfectly differentiated, which means that not only can the factorial plane be interpreted, but also each axis separately. In Fig. 4, the groups are identified with vectors and the species with points.

Multivariant Analysis. The first principal plane (Fig. 4) has the greatest explicative power (inertia rate of 89%); thus the most important differences among the study groups appear here. Axis 1 separates two periods of the community: summer and fall in the open pastureland. Spring in this same environment occupies an intermediate position.

Regarding axis 1, the three periods of the wooded pastureland are similar. (With respect to each axis, the figure should be interpreted by analyzing the relative position of the projection of the points on the axis, without taking into account the other dimension.)

In axis 2, the largest difference appears between spring in the open pastureland and summer in the wooded pastureland. However, for the purposes of this study, it is perhaps more relevant that the three periods in the open pastureland (projected onto axis 2) appear separated from the three periods in the wooded pastureland. Axis 2 explains 20% of the

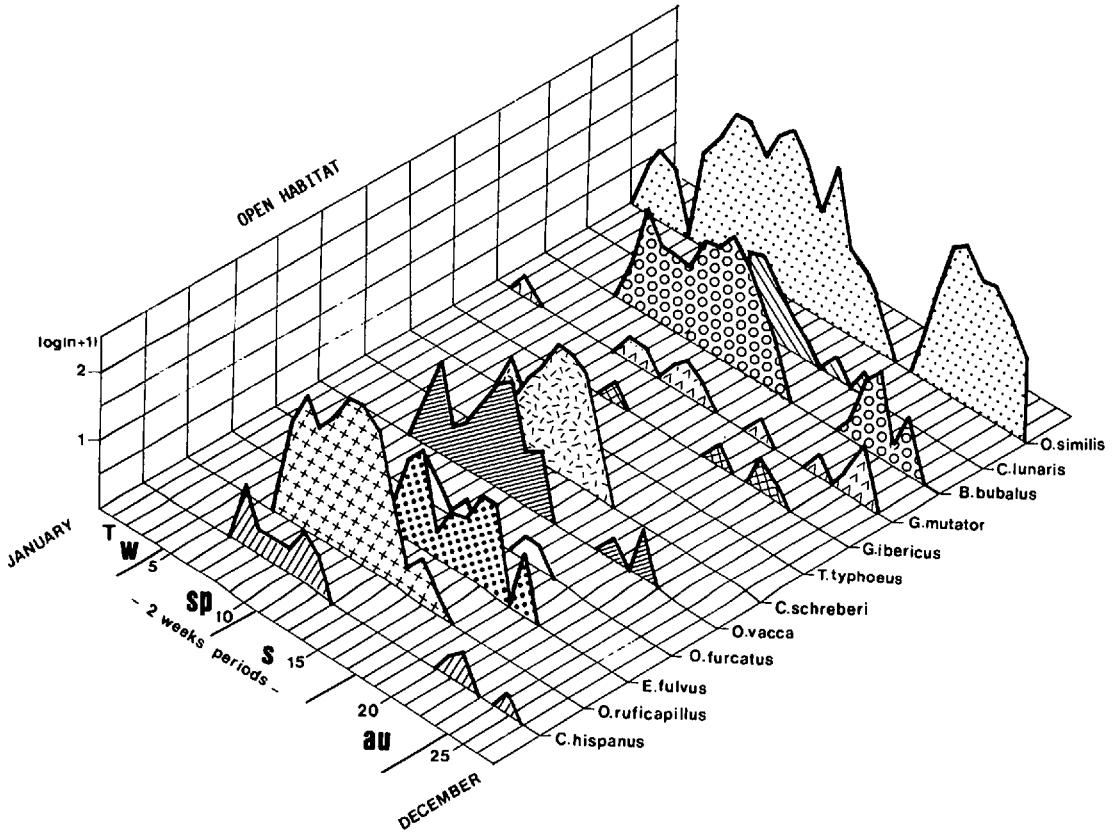

Fig. 2. Annual activity of the imagos of the most abundant species of Scarabaeidae and Geotrupidae in the open habitat (n, number of specimens; T, 2-wk periods; w, winter; sp, spring; s, summer; au, autumn).

inertia and axis 1 explains 68%, which means that the differences between two seasons in open pastureland are more marked than those appearing between the two communities (wooded and open pastureland). This does not imply, however, that the differences between the communities are less important.

The species with greatest contribution to axis 1, and therefore the most important for differentiating between summer and fall in the open pastureland, are *Onthophagus similis* (Scriba 1790), *O. vacca* (Linné 1767), *Caccobius schreberi* (Linné 1767) and *Euoniticellus fulvus* (Goeze 1777).

The species with greatest contribution to axis 2, and therefore the most important for differentiating between the two communities (wooded and open pastureland), are *Copris lunaris* (Linné 1758); *Bubas bubalus* (Olivier 1811); *Copris hispanus* (Linné 1764); *Typhaeus typhoeus* (Linné 1758); *Geotrupes mutator* Marsham 1802; *G. ibericus* Baraud 1958; and *O. ruficapillus* Brulle 1832.

Analysis of Communities. The separation of these communities of scarabs is due to the different composition, quantitative as well as qualitative, of the species in both environments (wooded and open pastureland). From observation of the plots obtained by representing the annual numerical variation of the different species (Fig. 2 and 3) and from the plot obtained by the application of the HJ-Biplot technique (Fig. 4), the species which characterize each community throughout the year can be deduced.

Open Pastureland. Contrary to what occurred in the wooded pastureland, the greatest number of species that characterize the open pastureland community were of small size and biomass (Fig. 2; Table 1). The greatest concentration of species occurred in the spring. At this time of year the community contained species which also appeared in summer or in fall. The predominant species in the spring, and the one characterizing this community at this time of year, was *O. ruficapillus*, as indicated in the information given by axis 2 on plane 1–2 (Fig. 4). This species was accompanied by *B. bubalus* and *O. vacca*, which were joined halfway through the season by *Caccobius schreberi* and *E. fulvus*, although the latter three species were important in the summer and not the spring. Small populations of *Copris lunaris* were also found in the spring, but neither they nor *B. bubalus* were important in the configuration of the community during this season.

During the summer the same species continued, although their numbers declined; only *E. fulvus*

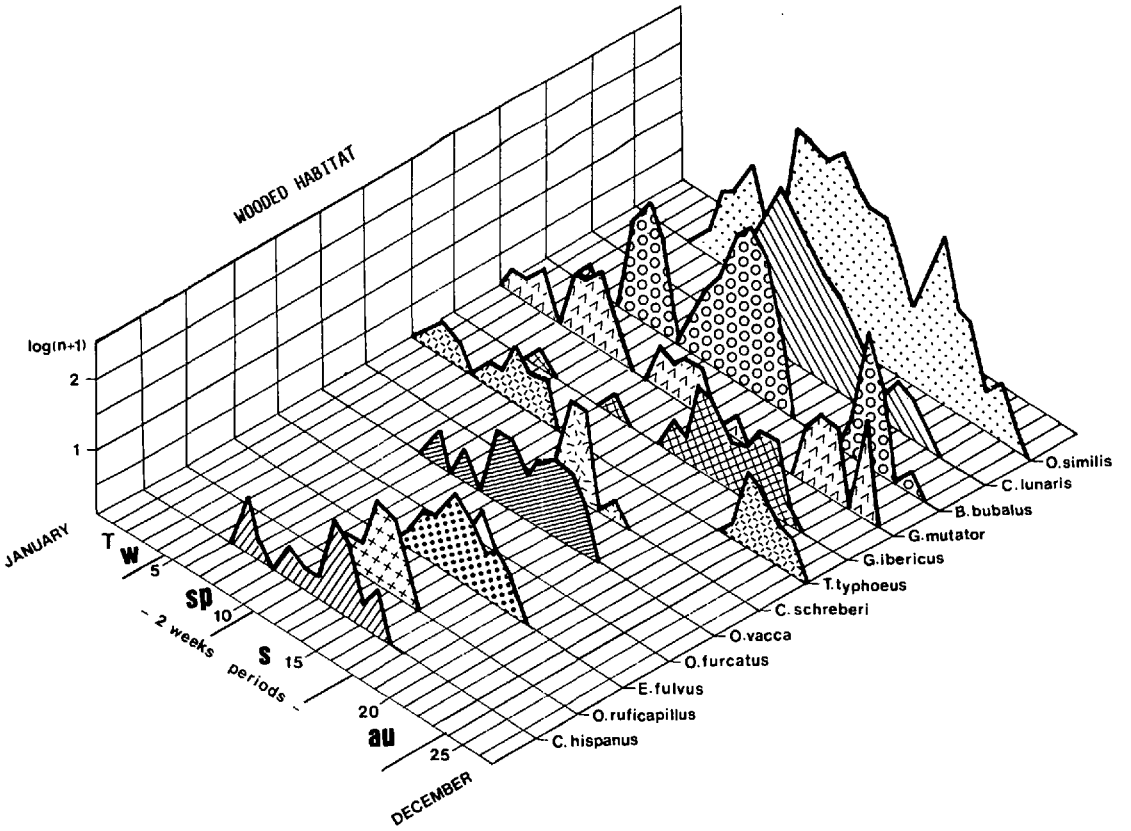

Fig. 3. Annual activity of the imagos of the most abundant species of Scarabaeidae and Geotrupidae in the wooded habitat (*n*, number of specimens; T, 2-wk periods; w, winter; sp, spring; s, summer; au, autumn).

remained abundant, followed by *O. vacca* and *Caccobius schreberi*, which mainly appeared in this season (Fig. 4).

Fall was the poorest season for species in open pastureland. *B. bubalus* reappeared, accompanied principally by some specimens of *G. mutator*.

Onthophagus similis was the most abundant and characteristic species during the entire year in open pastureland areas. It was especially important in the configuration of the open pastureland community in the fall (Fig. 4).

Wooded Pastureland. In the holm oak wooded areas the community was especially characterized by species of large size and biomass (Fig. 3; Table 1). This difference for the open pastureland areas was particularly pronounced during the summer. In summer the preponderant and characteristic species were *Copris lunaris* and *B. bubalus* (Fig. 4). Halfway through the summer *G. ibericus* (Fig. 4) appeared and its population was very important during the fall in wooded pastureland. The presence of *Copris hispanus* was also observed during the summer in wooded zones; its absence was characteristic of the open pastureland areas (Fig. 2 and 3).

The community in the holm oak wooded area was also very characteristic in the fall. Large species were observed in these areas; these either did not exist in the open pastureland area, as is the case of *T. typhoeus* (Fig. 2 and 3), or the number of specimens was much greater in the wooded areas and characterized them during the fall, as was the case of *B. bubalus* and *G. mutator*. The latter species was the most characteristic (Fig. 4). At the beginning of fall, *G. ibericus* also formed part of the community and its population was much greater and more important in the wooded area than in the open pastureland (Fig. 2 and 3).

During the spring, the wooded area and the open pastureland shared the presence of a species that was important for its biomass, *B. bubalus* (Table 1). Also present in both areas were *G. mutator* and *T. typhoeus*, although the quantitative importance of these two species was much greater in the wooded pastureland (Fig. 2 and 3). Also, one species which was only found in this environment in the spring was *O. coenobita* (Herbst 1783).

Discussion

It can be concluded that the habitat in which the droppings are deposited has a strong effect on the composition of the coprophagous fauna, coinciding with the findings of several authors (Mohr

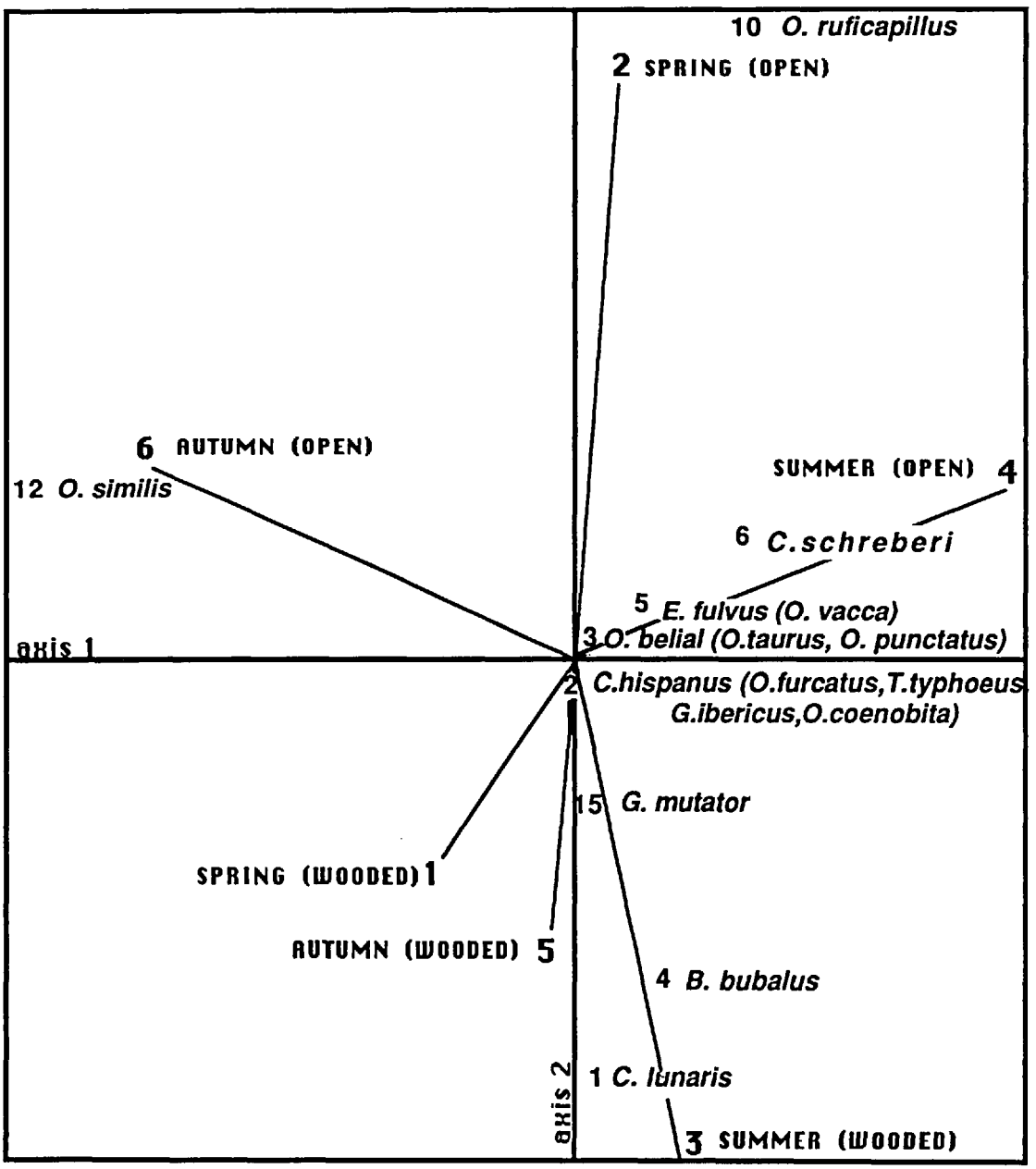

Fig. 4. Simultaneous HJ-Biplot representation: projection on plane 1–2. Selection of closeby points: Rows (=species): 2 (*C. hispanus*); 9 (*O. furcatus*); 14 (*T. typhoeus*); 16 (*G. ibericus*). Rows (=species): 3 (*O. belial*); 7 (*O. taurus*); 8 (*O. punctatus*); 11 (*O. coenobita*). Rows (=species): 5 (*E. fulvus*); 13 (*O. vacca*).

1943, Fincher et al. 1970, Merrit & Anderson 1977). The vegetational ground cover is an important factor in the distribution of dung-feeding scarabs (Howden & Nealis 1975, Oppenheimer 1977, Doube 1983, Lumaret & Kirk 1987). In our study we observed that the largest species have a clear preference for the wooded area (Fig. 2–4). This was especially evident during the summer and fall seasons. However, in the spring there was a large population of *B. bubalus* in the open pastureland, which decreased at the end of this season, but increased slightly in the wooded area. The increase in temperature and the decrease in air and soil humidity in the pasture area (Stanhill 1970, González-Bernáldez et al. 1975, Montoya 1982, Puerto et al. 1986) probably elicited a displacement of *B. bubalus* to the wooded areas. Therefore migration takes place on a spatial scale called "trivial range" (Southwood 1977), "limited area range" (Baker 1978), or "behavioral range" (Hanski 1980); and it occurs when the local conditions of the habitat change or as a response to feeding habits.

By contrast, the smaller species (*Onthophagus* spp., *Caccobius schreberi*, and *E. fulvus*) generally showed a greater preference for the open pastureland areas (Fig. 2–4), becoming very abundant in this habitat during the summer. Only *O. taurus* and *O. punctatus*, together with *Copris hispanus* and *O. furcatus* (F. 1781), do not seem to have special affinity for either of the two habitats. Only *Copris hispanus* seemed to settle more abundantly in the wooded areas, this being the habitat that it colonizes in summer probably due to the extreme dryness of the soil and the high temperatures prevailing in the open pastureland (González-Bernáldez et al. 1975, Puerto et al. 1986). Conversely, *O. furcatus* seemed to concentrate somewhat more in the open pastureland.

According to Lumaret (1980, 1983) and Lumaret & Kirk (1987), in the other areas of the Mediterranean Region, but in the places near the coast (Corsica and the Montpellier region in France), coprophagous fauna do not show a preference for wooded areas, but rather concentrate in areas of open pastureland. In other geographic regions, such as Texas (Fincher et al. 1986) and South Africa (Doube 1983), a larger concentration of species was observed in wooded areas. In the Salamanca region the wooded areas (holm oak) are composed of large expanses of *Q. rotundifolia* that form cleared "savannahlike" woodland called "dehesas." These wooded areas allow effective grazing and easy movement of the livestock because of the lack of underbrush. They are therefore areas with a great advantage for dung-feeding scarabs during times of drought and high temperatures, because there are better conditions of air and soil humidity, as well as less extreme temperatures beneath the trees. This habitat is also open enough to permit easy movement of dung-feeding scarabs and the colonization of droppings. These data, however, do not indicate that there is a fauna of dung-feeding scarabs exclusive to and specialized in wooded areas and another in open pastureland, as occurs in some latitudes (Howden & Nealis 1975, Walter 1978). Nevertheless, our findings point to a clear separation throughout the year between two communities of dung-feeding scarabs: one in wooded areas and the other in open pastureland. Most of the community in the wooded habitat is made up of species with large-sized beetles, whereas most of the community in the open habitat essentially comprises species with medium or small beetles. This undoubtedly has great consequences for the decomposition of cattle dung in both habitats, to the point where some cattle dung remains undegraded in the open pastureland areas in times of great drought. This problem already exists in some parts of the Salamanca area, as we observed in this study. It is very likely that the concentration of the species with the larger-sized beetles in the wooded areas is due to, as pointed out earlier, fewer thermal fluctuations throughout the day and the maintenance of a higher level of humidity. This means that the soil remains softer, which allows these scarabs to carry out their excavating activities more easily.

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