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BIODIVERSITY RESEARCH

Diversity, distinctiveness and conservation status of the Mediterranean coastal dung beetle assemblage in the Regional Natural Park of the Camargue (France)

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Abstract. The Mediterranean region as a whole has the highest dung beetle species richness within Europe. Natural coastal habitats in this region are among those which have suffered severe human disturbance. We studied dung beetle diversity and distinctiveness within one of the most important coastal protected areas in the west Euro-Mediterranean region (the regional Park of Camargue, southern France) and made comparisons of dung beetle assemblages with other nearby Mediterranean localities, as well as with other coastal protected area (Doñana National Park, Spain). Our finding showed that: (1) The species richness of coastal habitats in the Camargue is low and only grasslands showed a similar level of species richness and abundance to inland habitats of other Mediterranean localities. The unique habitats of the coastal area (beaches, dunes and marshes) are largely colonized by species widely distributed in the hinterland. (2) In spite of their low general distinctiveness, dune and marsh edges are characterized by the occurrence of two rare, vulnerable, specialized and large roller dung beetle species of the genus *Scarabaeus*. As with other Mediterranean localities, current findings suggest a recent decline of *Scarabaeus* populations and the general loss of coastal dung beetle communities in Camargue. (3) The comparison of dung beetle assemblages between the Camargue and Doñana shows that, in spite of the low local dung beetle species richness in the Camargue, the regional dung beetle diversity is similar between both protected areas. Unique historical and geographical factors can explain the convergence in regional diversity as well as the striking divergence in the composition of dung beetle assemblages between both territories.

Key words. Scarabaeoidea, dung beetles, insect coastal conservation, Mediterranean region, the Camargue, Doñana.

INTRODUCTION

The Mediterranean region represent one of the most ancient disturbed areas in Europe. For approximately 6000 years (dependent upon geographical location), Mediterranean ecosystems have been under the influence of human activities (Vernet & Thiébault, 1987; Reille *et al.*, 1996) which have contributed to their present multidimensional heterogeneity (di Castri, 1981). Throughout the long history of agropastoralism, the seminatural and pastoral ecotopes of open forests, shrublands, woodlands and grasslands, together with the agricultural ecotopes of patch- and hand-cultivated rock polycultures, have created a mosaic of landscapes (Naveh & Vernet, 1991). This mosaic of habitats extends into coastal areas, characterised by various environmental conditions such as aridity in sand dunes and humidity at the edges of marshes, combined with the omnipresence of salt and the occurrence of several soil textures. Traditionally, sheep and cattle grazing occurred on the hinterland and at the edges of coastal wet marshes, fertilizing these areas and giving dung beetle species (Coleoptera, Scarabaeoidea) the opportunity to extend and increase in abundance. Today, due to the development of mass tourism and its correlative urbanization (mainly in coastal areas), the seminatural habitats have become more and more patchily distributed, and many sandy habitats have changed or have been destroyed and grazing has declined.

The dung beetles include three families: Scarabaeidae, Aphodiidae and Geotrupidae. Geotrupidae and most of the Scarabaeidae (except Scarabaeini) species are tunnelers, digging vertical tunnels below the dung pat, and carrying dung into the bottom of the burrow. Scarabaeini are rollers, making and rolling away a ball of dung and digging a tunnel outside the dung pat. The small bodied Aphodiidae belong a third guild (the dwellers) as they feed and nest inside the dung pats. The decline of agropastoralism in the last few decades has led many species that were once very abundant at the beginning of 20th century to become very scarce (Johnson, 1962; Leclerc *et al.*, 1980; Lumaret, 1990; Väisänen & Rassi, 1990; Biström *et al.*, 1991; Lumaret & Kirk, 1991; Miessen, 1997; Lobo, 2001). Coastal dung beetle assemblages are very sensitive to human disturbance, especially when these disturbances have impacted upon Mediterranean biotopes inhabited for rare and localized species (Pyle *et al.*, 1981; Balleto & Casale, 1991; Gray, 1991). In the case of dung beetles, alteration of most of the coastal biotopes of the west Mediterranean area since the 1960s has strongly affected many roller populations, reducing the size of their range, with a consequent decrease of species richness (Lobo, 2001).

The aims of the present paper are to (i) establish the current dung beetle fauna composition and species richness of the Regional Park of Camargue (southern France), one of the most important protected coastal areas in the west Euro-Mediterranean region; (ii) estimate the dung beetle diversity and the faunal distinctiveness of this area with regard both to nearby Mediterranean localities and to other Mediterranean coastal area with similar characteristics; and (iii) make a preliminary evaluation of the current conservation status of the Camargue dung beetle species.

To carry out these objectives, the dung beetle assemblages of coastal habitats of the Camargue will firstly be reviewed to estimate the species diversity and to identify the most uncommon and specialized species, as well as to identify their preferred habitats (local scale analysis). Subsequently, the specificity of the coastal dung beetle fauna in the Camargue will be compared with the fauna of the hinterland (regional scale analysis). Then, the species richness and composition of the dung beetle fauna of the Camargue will be compared to that of the Doñana National Park in Spain (Lobo *et al.*, 1997b), which is the other important protected coastal territory located in the western Mediterranean region (interregional scale analysis). The results of these studies were used to estimate the probable current conservation status of coastal dung beetle species within the Camargue.

MATERIALS AND METHODS

Dung beetle information

Local scale

Dung beetles were trapped from 10 May to 19 June 1996 in seven coastal localities in the Camargue (Fig. 1). These constituted a representative transect that covered the major coastal habitats, from seaside to inland. Six distinct habitats were identified and sampled, namely beach, pre-dune, dune, marsh, forest and grassland habitats (Table 1). There were good weather conditions (i.e. low wind, and sun) throughout the sampling period. Pitfall traps baited with dung were used to collect beetles. Each trap consisted of a plastic basin 210 mm in diameter containing a preserving fluid (a water–liquid soap mixture) and buried to its rim in the soil. Fresh cattle dung (*c.* 350 g) was placed on a wire grill on the top of the basin. All the pitfall traps were exposed only once during the trapping period. The sampling effort (number of pitfall traps per habitat) was roughly proportional to the habitat area (between 3 and 58 traps per habitat). In total, 115 baited pitfall traps were set up. A small number of traps attracted the beetles within 24 h ($n = 30$), whilst most traps were in position for 48 hours before beetles were caught. The mean distance between the pitfall traps within a locality was *c.* 10 m.

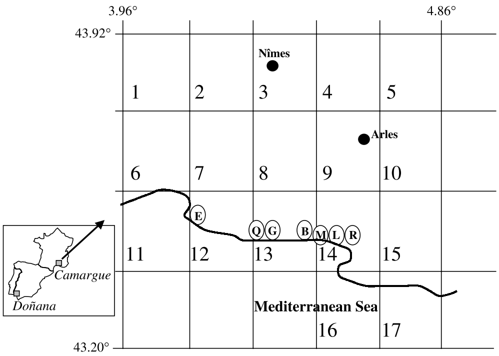

Fig. 1 Location of the seven sample sites in southern France. E: Espiguette; Q: Quatre Maries; G: Grand Radeau; B: Baisse de Mouillot; M: Montille de Charles; L: Longue Montille; R: Radeau de la Foux Vieille. The Mediterranean region, which included the whole of the Camargue area was divided into 17 squares of 0.18° × 0.18° (approximately 304 km^2). Insert shows the relative positions of the Camargue (France) and the Doñana Park (Spain) compared in the interregional scale analysis.

The sampling undertaken at a local scale is evidently not comprehensive. However, due to the adaptation of dung beetles to colonize highly patchy and ephemeral resources, baited pitfall traps allow us to collect the representative species of each habitat, thus making the estimation of species richness feasible. The efficiency of this model of trapping has been tested previously (Lobo *et al.*, 1988; Veiga *et al.*, 1989), and has shown that these traps do not need to be in position for a long time to capture the fauna associated with dung; the difference between trapping over 24 or 48 h being minimal. Moreover, in the Mediterranean, only a few dung-baited pitfall traps are needed to give a good picture of the structure and composition of local dung beetle assemblages. Lobo *et al.* (1998) demonstrated that 15 traps allowed the collection of 95% of the species present within a *c.* 1 km^2 localitiy, and that only 2 traps resulted in the collection of 53% of species; in terms of total dung beetle abundance and biomass, these species accounted for *c.* 85% of the complete inventory. With regard to the effect of season on sampling, previous studies have shown that the dung beetle inventory of a local assemblage when recorded in spring ranged from 70% to 80% of the complete annual inventory (Martín-Piera *et al.*, 1992; Lobo & Martín-Piera, 1993; Lobo *et al.*, 1997b). To test if the total number of trapped species was an underestimate of the true species richness along the transect, we calculated the species accumulation curve, i.e. the cumulative number of recorded species as a function of the randomised number of pitfall traps (Colwell & Coddington, 1995). For this analysis, the EstimateS statistical software package (Colwell, 1997) was used. To eliminate the effect of pitfall trap order, 100 randomizations of the pitfall order were computed. With the sampling effort accomplished, a clearly asymptotic richness score was obtained. With only 28 pitfall traps, 82% of total species richness was recorded; while with 40 traps, 91% was recorded. The ceiling value of the asymptotic curve is obtained with 87 pitfall traps; at this level we can have some confidence in the quality of the faunal and species richness information provided by the transect.

Table 1 Coastal habitats sampled in each locality of the Camargue; abbreviations as in Fig. 1

		Habitats						Number of pitfall-traps
		Beach	Pre-dune	Dune	Marsh	Forest	Grassland	
Espiguette	E	×	×	×	×	×		58
Longue Montille	L			×				3
Montille de Charles	M			×				3
Baisse de Mouillot	B			×				3
Grand Radeau	G			×			×	6
Quatre Maries	Q			×		×		6
Radeau de la Foux Vieille	R			×	×			36
Total								115

Regional scale

The survey of the Camargue dung beetle fauna (local study) was extended to the surrounding area, which included the whole of the Camargue. The total surrounding area was about 5316 km^2 and ranged from 43.20°N to 43.92°N and from 3.96°E to 4.86°E (Fig. 1). This area was divided into 17 squares of 0.18° × 0.18° (each approximately 304 km^2). A prerequisite for any faunal comparison between sites is that their inventories are reasonably complete. This requires us to have a measure of the sampling effort at each site, and as this is frequently lacking, between-study comparisons are often tentative (Gaston, 1996). Despite the lack of sampling effort measurements, one can attempt to describe the main regional patterns in species richness variation using information based on national atlases, assuming that unevenness in sampling effort does not completely obscure any regional pattern in species richness. In our case, the exhaustive information contained within the French Scarabaeoidea Laparosticti data base (Lumaret, 1990), which contains all the available information about these species, together with a detailed spatial analysis (Lobo *et al.*, 1997a), was used to estimate the species composition in each square. According their distance from the coastline, squares were ranked into a coastal subregion (numbers 6, 7, 11, 12, 13, 14, 15, 16 and 17) or into a hinterland subregion (numbers 1, 2, 3, 4, 5, 8, 9 and 10) (Fig. 1). The species composition, species richness and species rarity in the two subregions were estimated. Species rarity was calculated as $1 - (n_i/n)$; where n_i was the number of coastal or hinterland squares where the species i was present, and n was the total number of coastal or hinterland squares (9 and 8, respectively).

Inter-regional scale

The Doñana National Park (Spain) and the Regional Natural Park of the Camargue (France) are protected areas, considered as wildlife sanctuaries, and are highly representative of southern European coastal habitats. These two estuaries are quite similar from an ecological point of view, although they are 1200 km apart: Doñana is located 37°N and 7°W on the Atlantic shore, whereas the Camargue is located 43.5°N and 4.5°E on the Mediterranean coast (Fig. 1). Both sites are of particular interest for dung beetles because they have a rich mammal fauna made up of wild boar, deer, rabbit, hare, cattle and horse in Doñana and of wild boar, rabbit, cattle and horse in the Camargue. The dung beetle faunas of the Camargue and Doñana were compared using the data presented here and those published by Lobo *et al.* (1997b).

Data analysis

Taking into account the rectangular matrix of species abundance in the pitfall traps, a Principal Component Analysis (PCA) has been used in the analysis of the local data to detect the structure in the relationship among species (Legendre & Legendre, 1998). Free distribution statistical tests (Siegel & Castellan, 1988) were used to test for significant differences between independent groups (Kruskal–Wallis ANOVA by ranks test) and to express the relationship between two variables (Spearman rank correlation coefficient).

RESULTS

Local scale analysis

Trapping results are surprisingly poor. A high proportion (43.5%) of the total pitfall traps did not contain any specimens (50 of 115 pitfall traps) and only 337 individuals of 11 species were collected in the seven coastal localities of the Camargue (Table 2). Although these results should be considered carefully, we believe that the low number of species recorded is not due to insufficient sampling effort, because most of spring sampling programmes in the Mediterranean allowed us to collect many more species with much less sampling effort (see Discussion).

Collected dung beetles belonged to the families Scarabaeidae (9 species) and Aphodiidae (2 species). Geotrupidae were not observed. Both the number of species and the number of individuals per trap were significantly different for the six habitats under consideration (Kruskal–Wallis test (KW) for species = 13.42, $P = 0.02$; KW for individuals = 11.61, $P = 0.04$). However, if grassland data were excluded from the comparison, no difference was observed between habitats for either the number of species ($KW = 4.05$, $P = 0.40$) or the number of individuals ($KW = 2.16$, $P = 0.71$). Both species richness and abundance are higher

Table 2 Mean abundance per pitfall trap of dung beetle species collected in each one of the coastal habitats of the Camargue. KW is the Kruskal–Wallis ANOVA by ranks, which was used to test if the probability of species occurrence is higher in some habitat. N = number of individuals, S = number of species, NS = not significant, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

	Beach	Pre-dune	Dune	Marsh	Forest	Grassland	Total	Total N	KW
Scarabaeus sacer L.	0.00	0.00	0.16	0.19	0.00	0.00	0.10	12	5.2 ns
S. semipunctatus F.	0.00	0.00	0.16	0.00	0.00	0.00	0.07	8	8.6 ns
Euoniticellus fulvus (Goeze)	0.00	0.00	0.02	0.00	0.00	2.33	0.07	8	28.4***
E. pallipes (F.)	0.00	0.00	0.00	0.10	0.00	1.33	0.05	6	23.9***
Onthophagus emarginatus Muls.	0.00	0.00	0.06	0.05	0.83	0.00	0.12	14	41.0***
O. furcatus (F.)	0.00	0.00	0.00	0.00	0.00	2.33	0.06	7	42.0***
O. nuchicornis (L.)	0.86	1.11	0.27	0.29	0.08	4.67	0.54	62	30.1***
O. taurus (Schreb.)	0.00	0.00	0.04	0.24	0.17	2.00	0.13	15	14.0*
O. vacca (L.)	0.05	0.00	0.24	0.24	0.08	11.00	0.45	52	17.1**
Aphodius ghardimaouensis Balth.	0.00	0.00	0.04	0.19	0.00	0.00	0.05	6	8.6 ns
A. haemorrhoidalis (L.)	0.00	0.00	1.04	0.05	0.00	31.67	1.28	147	24.8***
Total	0.91	1.11	2.04	1.33	1.17	55.33	2.93		
N	19	10	100	28	14	166		337	
S	2	1	9	8	4	7	11		
S per trap	0.48	0.56	0.80	1.01	0.75	5.67	0.91		
Number of pitfall traps	21	9	49	21	12	3	115		

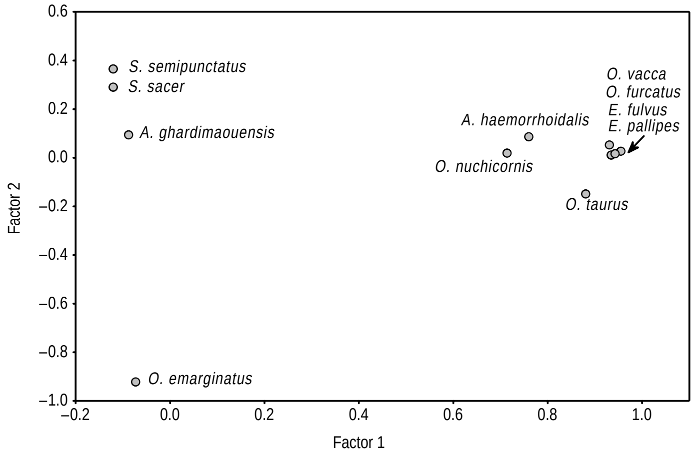

Fig. 2 Two-dimensional scatterplot of the factor loadings after performing a Principal Component Analysis that took into account the rectangular matrix of species abundance in pitfall traps (local scale analysis).

in the grassland (5.7 species and 55.3 individuals per pitfall trap) than in the five other habitats (Table 2). The dung beetle assemblages of beach, pre-dune, dune, marsh and forest were equally species poor (between 0.5 and 1.0 species per pitfall trap).

Except for *Onthophagus emarginatus*, whose mean abundance by trap was higher in the forest, all the remaining species which showed a significant Kruskal–Wallis test score had their highest mean abundance per trap in the grassland habitat (Table 2). In addition, *Onthophagus nuchicornis* showed a moderate population level in the beach and pre-dune, *O. taurus* in the forest and marsh site, and *Aphodius haemorrhoidalis* in the sand dune. The three species that did not show a preference for any habitat (*Scarabaeus sacer*, *S. semipunctatus* and *A. ghardimaouensis*) were only present in the dune and marsh habitats, but with low densities.

The first and second factors of the PCA account for 49.5% and 10.5% of variance, respectively. The two-dimensional scatterplot of these factor loadings (Fig. 2) shows two groups of species: one group includes those species that prefer grassland habitats (positive scores of factor 1), and the other group includes the remaining coastal species, which prefer other coastal habitats. In the first group, factor 1 discriminates the grassland species with low population levels in other habitats (*O. nuchicornis*, *O. taurus* and *A. haemorrhoidalis*); factor 2 discriminates three species only present in dune or marsh habitats (*S. sacer*, *S. semipunctatus* and *A. ghardimauensis*) from the species that occurs mainly in forest (*O. emarginatus*).

Regional scale analysis

The numbers of species in the coastal and hinterland subregions are similar (76 and 79, respectively) as well as the species composition of both subregions (Table 3). Sixty-six species (74.1% of the total) occur simultaneously in both subregions and only 10 and 13 species occur exclusively in the coastal or hinterland squares, respectively. The rarity scores of species in coastal and hinterland subregions are highly correlated (Spearman rank correlation coefficient, $r_s = 0.655$; $P < 0.00001$). Hence, generally the rarest species in coastal squares are also the rarest ones in hinterland squares. Rarity scores are high for the exclusive species of coastal squares (mean = 0.80 ± 0.11 SD; range = 0.56–0.89), as well as for the species occurring exclusively in hinterland squares (0.85 ± 0.06; range = 0.75–0.88) (Table 3). The absolute difference in the rarity scores between both subregions (RAD) shows that 89.9% of all species (80 species) have rarity differences of less than 0.40 (Fig. 3) and that only 9 species have RAD scores higher or equal to 0.40 (Table 3). Only *Scarabaeus sacer* occurs exclusively in the coastal subregion and in some places can be considered common (rarity = 0.56). Moreover, *S. semipunctatus* is the only species that is very rare in the hinterland (rarity = 0.88), while it can

Table 3 Absent (0) and present (1) species in the coastal 0.18° × 0.18° squares (numbers 6, 7, 11, 12, 13, 14, 15, 16 and 17 in Fig. 1) and in hinterland squares (numbers 1, 2, 3, 4, 5, 8, 9 and 10) of the Camargue region. The rarity score of species in each subregion was calculated as $1-(n_i/n)$; where n_i is the number of coastal or hinterland squares in which the species i is present, and n is the total number of coastal or hinterland squares (9 and 8, respectively). RAD is the absolute difference between the coastal and hinterland species rarity scores. *species with RAD scores higher or equal to 0.40

	Coastal squares		Hinterland squares		RAD
		Rarity		Rarity	
Scarabaeidae: 34 species					
Scarabaeus laticollis L. (1767)	0	1.00	1	0.88	0.13
S. pius (Illiger), 1893	0	1.00	1	0.88	0.13
S. sacer L., 1758*	1	0.56	0	1.00	0.44
S. semipunctatus Fabricius, 1792*	1	0.33	1	0.88	0.54
Sisyphus schaefferi (L.), 1758	0	1.00	1	0.75	0.25
Gymnopleurus flagellatus (Fabricius), 1787	1	0.56	1	0.63	0.07
G. mopsus (Pallas), 1781	1	0.89	1	0.75	0.14
G. sturmi Mac Leay, 1821	1	0.78	1	0.63	0.15
Copris hispanus (L.),1764	1	0.44	1	0.25	0.19
C. lunaris (L.), 1758	1	0.78	1	0.75	0.03
Onitis belial Fabricius, 1798	1	0.78	1	0.88	0.10
Bubas bison (L.), 1767	1	0.44	1	0.75	0.31
B. bubalus Olivier, 1811	1	0.33	1	0.25	0.08
Euoniticellus fulvus (Goeze), 1777	1	0.22	1	0.38	0.15
E. pallipes (Fabricius), 1781	1	0.33	1	0.63	0.29
Caccobius schreberi (L.), 1767*	1	0.67	1	0.25	0.42
Euonthophagus amyntas (Olivier), 1789*	1	0.78	1	0.13	0.65
Onthophagus coenobita (Herbst), 1783	1	0.44	1	0.25	0.19
O. emarginatus Mulsant, 1842	1	0.33	1	0.00	0.33
O. furcatus (Fabricius), 1781	1	0.33	1	0.13	0.21
O. grossepunctatus (Reitter), 1905	1	0.89	1	0.63	0.26
O. illyricus (Scopoli), 1763*	1	0.78	1	0.38	0.40
O. joannae Goljan, 1953	1	0.78	0	1.00	0.22
O. lemur (Fabricius), 1781*	1	0.78	1	0.38	0.40
O. maki (Illiger), 1803	1	0.89	1	0.75	0.14
O. nuchicornis (L.), 1758	1	0.22	1	0.38	0.15
O. opacicollis Reitter, 1893	1	0.67	1	0.38	0.29
O. ovatus (L.), 1767	1	0.33	1	0.00	0.33
O. ruficapillus Brullé, 1832	1	0.33	1	0.25	0.08
O. semicornis (Panzer), 1798	1	0.89	1	0.63	0.26
O. similis (Scriba), 1790	0	1.00	1	0.88	0.13
O. taurus (Schreber), 1759	1	0.22	1	0.00	0.22
O. vacca (L.), 1767	1	0.22	1	0.00	0.22
O. verticicornis (Laicharting), 1781	1	0.89	0	1.00	0.11
Total	30		31		
Aphodiidae: 49 species					
Aphodius biguttatus Germar, 1824	0	1.00	1	0.75	0.25
A. bonnairei Reitter, 1892*	1	0.78	1	0.25	0.53
A. brevis Erichson, 1848	1	0.89	1	1.00	0.11
A. cervorum Fairmaire, 1871	0	1.00	0	0.88	0.13
A. consputus Creutzer, 1799	1	0.56	1	0.63	0.07
A. constans Duftschmid, 1805	1	0.67	1	0.38	0.29
A. contaminatus (Herbst), 1783	1	0.67	1	1.00	0.33
A. distinctus (Muller), 1776	1	0.44	0	0.50	0.06
A. elevatus (Olivier), 1789	1	0.56	1	0.50	0.06
A. erraticus (L.), 1758	1	0.56	1	0.25	0.31

Table 3 *continued.*

	Coastal squares		Hinterland squares		RAD
		Rarity		Rarity	
A. fimetarius (L.), 1758	1	0.44	1	0.38	0.07
A. foetens (Fabricius), 1787	1	0.89	1	1.00	0.11
A. foetidus (Herbst), 1783	1	0.22	0	0.38	0.15
A. fossor (L.), 1758	0	1.00	1	0.88	0.13
A. ghardimaouensis Balthasar, 1929	1	0.33	1	0.63	0.29
A. granarius (L.), 1767	1	0.22	1	0.13	0.10
A. haemorrhoidalis (L.), 1758	1	0.22	1	0.50	0.28
A. ictericus (Laicharting), 1781	1	0.78	1	1.00	0.22
A. immundus Creutzer, 1799	1	0.44	0	0.63	0.18
A. lineolatus Illiger, 1803	0	1.00	1	0.88	0.13
A. lividus (Olivier), 1789	1	0.33	1	0.63	0.29
A. lugens Creutzer, 1799	1	0.56	1	0.63	0.07
A. luridus (Fabricius), 1775*	1	0.56	1	0.00	0.56
A. maculatus Sturm, 1800	0	1.00	1	0.88	0.13
A. melanostictus Schmidt, 1840	0	1.00	1	0.88	0.13
A. merdarius (Fabricius), 1775	1	0.44	1	0.25	0.19
A. obliteratus Panzer, 1823	1	0.89	1	0.88	0.01
A. paracoenosus Balthasar & Hrubant, 1960	1	0.33	1	0.13	0.21
A. plagiatus (L.), 1767	1	0.56	1	0.50	0.06
A. porcus (Fabricius), 1792	1	0.67	1	0.75	0.08
A. prodromus (Braham), 1790	1	0.33	1	0.38	0.04
A. pusillus (Herbst), 1789	1	0.78	1	1.00	0.22
A. quadriguttatus (Herbst), 1783	1	0.78	0	0.50	0.28
A. quadrimaculatus (L.), 1761	1	0.89	1	0.75	0.14
A. reyi Reitter, 1892	1	0.89	1	0.88	0.01
A. satellitius (Herbst), 1789	1	0.44	1	0.25	0.19
A. scrofa (Fabricius), 1787	1	0.67	1	0.38	0.29
A. scrutator (Herbst), 1789	1	0.44	1	0.75	0.31
A. sordidus (Fabricius), 1775	1	0.89	1	1.00	0.11
A. sphacelatus (Panzer), 1798	1	0.56	0	0.75	0.19
A. striatulus Waltl, 1835	1	0.89	1	1.00	0.11
A. sturmi Harold, 1870	1	0.44	0	0.63	0.18
A. suarius Faldermann, 1835	1	0.67	1	0.75	0.08
A. subterraneus (L.), 1758	1	0.33	1	0.50	0.17
A. thermicola Sturm, 1800	0	1.00	1	0.88	0.13
A. tingens Reitter, 1892	1	0.44	1	0.38	0.07
A. varians Duftschmid, 1805	1	0.44	1	0.50	0.06
A. vitellinus Klug, 1845	1	0.89	1	0.88	0.01
Euheptaulacus carinatus (Germar), 1824	1	0.89	1	0.88	0.01
Total	42		42		
Geotrupidae: 6 species					
Geotrupes mutator Marsham, 1802	1	0.89	1	0.63	0.26
G. spiniger Marsham, 1802	1	0.33	1	0.50	0.17
Sericotrupes niger (Marsham), 1802	1	0.89	1	0.63	0.26
Thorectes intermedius (Costa), 1827	0	1.00	1	0.75	0.25
Trypocopris vernalis fauveli Bedel	0	1.00	1	0.88	0.13
Typhaeus typhoeus (L.), 1758*	1	0.89	1	0.38	0.51
Total	4		6		
Total species	76		79		
Exclusive species	10		13		

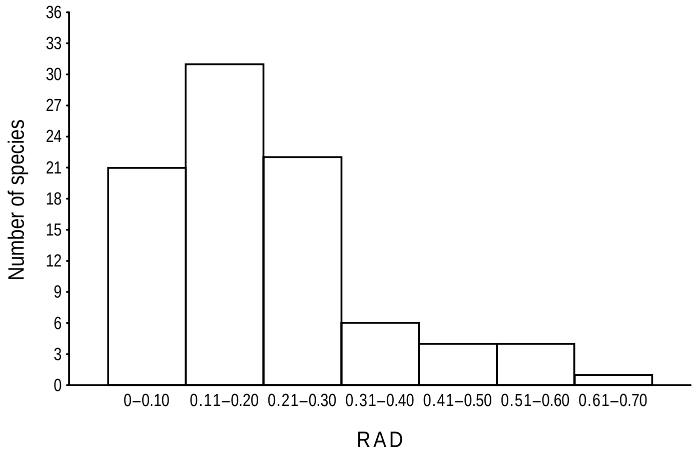

Fig. 3 Distribution of the RAD scores for the 89 dung beetle species (Table 3) of the region under study (Fig. 1). RAD is the absolute difference in species rarity score between the coastal and hinterland subregions, where the species rarity for each subregion was calculated as $1 - (n_i/n)$; n_i is the number of coastal or hinterland squares in which the species is present, and n is the total number of coastal or hinterland squares.

be considered as a relatively common species in the coastal subregion (rarity = 0.33). *Caccobius schreberi*, *Euonthophagus amyntas*, *Onthophagus illyricus*, *O. lemur*, *Aphodius bonnairei*, *A. luridus* and *Typhaeus typhoeus* are all common species in the hinterland subregion but are rare in the coastal squares (Table 3).

Inter-regional scale analysis

The dung beetle fauna of the Camargue *sensu stricto* (squares number 8, 9, and 12–17 in Fig. 1) was slightly richer than the fauna of Doñana: 72 and 65 species were recorded in the two regions, respectively (Table 4). This difference was mostly due to the Aphodiidae family (39 and 32 species in the Camargue and Doñana, respectively) whereas the number of Scarabaeidae and Geotrupidae species were similar between the two regions. Of the Scarabaeidae, 45% occur simultaneously in both regions. Conversely, 90% of Geotrupidae species were restricted to one or other of the regions. Aphodiidae showed an intermediate distribution, with 34% of species in common (Table 4). When the three families were considered together, 50% and 45% of dung beetle species recorded in the Camargue and in Doñana, respectively, were not found in the other coastal region. However, 94% of species peculiar to the Camargue were also observed in the Iberian Peninsula, whereas 76% of species peculiar to Doñana do not occur in continental France (Table 4).

DISCUSSION

The dung beetle species richness of the different coastal habitats of the Camargue is generally low, with only the grassland assemblage showing a high species richness and abundance of individuals. Such low species richness in comparison to the adjacent inland territories is not surprising and has also been described in coastal areas of southern Spain (Lobo *et al.*, 1997b). The coastal grassland habitat assemblage was numerically the most species rich, but it was made up of common species widely distributed in the whole area. Thus, the highest population levels of nearly all the Camargue species were observed within grasslands, although a few species might colonize coastal habitats from inland source populations. Beach and pre-dune habitats were colonized by two species, *Onthophagus nuchicornis* and *O. vacca*, which were common and abundant in the grassland habitats and widely distributed within the region. On the other hand, dune, marsh and, to a lesser extent, forest habitats were home to species poor but very uncommon communities,

Table 4 Faunal comparison of the Camargue and Doñana. The two lists correspond to the species present in only one of the two territories. Underlined: species of each territory which are absent in the Iberian Peninsula or in continental France. Asterisk: species particularly rare in France (according to Lumaret, 1990)

	Camargue			Doñana	
	Total number of species	Number of exclusive species	Number of species incommon	Number of exclusive species	Total number of species
Scarabaeidae	28	11	17	10	27
Aphodiinae	39	21	18	14	32
Geotrupinae	5	4	1	5	6
	Scarabaeus semipunctatus	*A. scrofa*		*Scarabaeus cicatricosus*	*A. mayeri*
	Copris lunaris	*A. subterraneus*		*Onitis ion**	*A. lineolatus*
	Euonthophagus amyntas	*A. quadrimaculatus*		*Chironitis hungaricus* *	*A. castaneus*
	Onthophagus coenobita	*A. foetens*		*Euoniticellus pallens*	*A. striatulus*
	O. lemur	*A. suarius*		*Onthophagus punctatus*	*A. longispina*
	O. nuchicornis	*A. constans*		*O. similis*	*A. cognatus*
	O. illyricus	*A. sordidus*		*O. marginalis*	*A. tersus*
	O. emarginatus	*A. pusillus*		*O. melitaeus*	*A. unicolor**
	O. grossepunctatus	*A. obliteratus*		*O. hirtus*	*A. lusitanicus*
	O. ovatus	*A. contaminatus*		*O. latigena*	*A. villareali*
	O. joannae	*A. distinctus*		*Heptaulacus algarbiensis*	*Typhaeus momus*
	Aphodius consputus	*A. prodromus*		*H. brancoi*	*Ceratophyus hoffmannseggi*
	A. lugens	*A. paracoenosus*		*Aphodius baraudi*	*Geotrupes ibericus*
	A. plagiatus	*A. reyi*		*A. hydrochaeris**	*Thorectes hispanus*
	A. varians	*Typhaeus typhoeus*			*Th. laevigatus*
	A. bonnairei	*Geotrupes mutator*			
	A. porcus	*G. spiniger*			
	A. scrutator	*Thorectes intermedius*			

although they consisted of species widely distributed in the inland part of the Camargue (*Onthophagus emarginatus* in the woody parts of the coastal area, and *Aphodius ghardimaouensis* restricted to marsh and dune habitats). The occurrence of *O. emarginatus* is generally restricted to dry, open landscapes where this species exploits rabbit's pellets (Lumaret, 1978–79b 1990; Jay-Robert, 1997). In the present study, the obvious preference of *O. emarginatus* for the forested habitat may be due to higher rabbit densities in the forest which has stable and relatively dry sandy soils, compared to the constantly moving dunes of the seaside and the inland marshes or open field habitats which often flood during winter. The presence of *A. ghardimaouensis* exclusively in dune and marsh habitats is easier to explain because this species prefers dry soils (Lumaret, 1990); in the coastal area, the clay marshes, which were dry during our sampling period, and the sandy dunes offered these conditions.

The comparison of coastal and hinterland assemblages in the Camargue shows that most of species found in coastal habitats are widely distributed in the hinterland and that species exclusive to coastal habitats are rare. Moreover, the interregional comparison shows that 95% of the species recorded only in the Camargue (i.e. absent in Doñana) are widely distributed in France and Europe. In France, only *Scarabaeus sacer* and *S. semipunctatus* can be considered as coastal species. *Scarabaeus sacer* was exclusive to the dune and marsh habitats of the eastern part of the Camargue, while *S. semipunctatus* was strictly confined to the dune habitat. In southern France, the strictly coastal distribution of these two *Scarabaeus* species has been reported many times. *Scarabaeus sacer* is known to prefer the sandy-silt laden soils covering the back-dune (Lumaret & Kirk, 1987; Lumaret, 1990), while *S. semipunctatus* is confined to sandy dunes (Thérond & Bigot, 1964; Dajoz, 1972; Lumaret, 1978–79a). This last species is also the most striking element of communities of the sandy coast habitats on the Iberian Peninsula (Lobo & Martín-Piera, 1993). On the Atlantic sandy coast of the Iberian Peninsula (particularly in Doñana), *S. semipunctatus* is replaced by a vicariant *Scarabaeus* species (*S. cicatricosus*) (Lobo *et al.*, 1997b).

One can characterize coastal areas such as the Camargue by their low distinctiveness with regard to inland areas, but also by the specific occurrence of some vulnerable and large-sized species (between 20 and 30 mm). Rollers in Mediterranean countries are in constant decline, probably due to the degradation of coastal habitats by humans (Lobo, 2001). The recent decline of the Camargue *Scarabaeus* populations is indicated by the results of the present study. Only 12 and 8 specimens of *S. sacer* and *S. semipunctatus*, respectively, were collected in spite of the high sampling effort in their preferred habitats (49 traps in the dune habitat and 21 in the marsh habitat sampled within the protected area of the National Reserve of the Camargue, situated in the largest dune area of the French Mediterranean border). Whereas, 25 years ago, in the same area (the Espiguette dunes) and within 4 days, Dajoz (1972) caught 364 specimens of *S. semipunctatus*. Using the capture–recapture method, this author estimated the population density to be around 100 specimens per ha. Currently, along the whole French Mediterranean coast, the two *Scarabaeus* species show a patchy and irregular distribution. *Scarabaeus sacer* is present in only two sites, one close to the Spanish boundary and the other in the Camargue. *Scarabaeus semipunctatus*, which occurred previously all along the French sandy coast from Italy to Spain, became very scarce recently, in particular in the eastern part of the Rhône river (Lumaret, 1990).

The current conservation status of dung beetles in the Camargue region can be estimated from some additional results. The inventory of the dung beetle species of the Camargue comprises 72 species, 70% of all species recorded in the Languedoc administrative region (Lumaret & Kirk, 1991). Although this regional species richness is close to that of Doñana (65 species), the local species richness, as well as the mean abundance and the mean number of species per trap, is surprisingly low. Exhaustive sampling using 115 baited pitfall traps only recorded 337 individuals (2.9 individuals per trap) belonging to 11 species, representing *c.* 15% of the total species pool potentially present in the Camargue. Although further sampling is required to obtain more conclusive results, this paucity of species does not appear to be the result of insufficient sampling. A spring sampling programme carried out by Lobo *et al.* (1997b) in eight coastal habitats of the National Park of Doñana using 24 pitfall traps similar to those used in the Camargue collected 7991 individuals in total, belonging to 41 species (333 beetles per trap); and 1610 individuals belonging to 21 species were trapped in the dune habitat using only six pitfall traps (268 beetles per trap). In pasturelands of the Iberian Peninsula, the average dung beetle species richness per pitfall trap in spring is usually relatively constant, ranging from 12 to 14 species (Lobo *et al.*, 1988; Veiga *et al.*, 1989; Hortal-Muñoz *et al.*, 2000). In the Causse Méjean (southern France), 15 pitfall traps at 10-m intervals in grasslands recorded between 17 and 34 dung beetle species according to grazing intensity, with a mean richness per trap of 7 to 18 species, and an mean abundance of 33 to 578 individuals per trap (Kadiri *et al.*, 1997). Finally, 25 pitfall traps set up in six grasslands in the Garrigues region close to Montpellier (75 km from the Camargue) recorded between 27 and 34 species, with a mean abundance per trap of 48 to 373 individuals and a mean richness per trap of 14 to 21 species (Lobo *et al.*, 1998).

Hence, today coastal dung beetle assemblages in the Camargue have probably become very poor. If the two main taxonomic groups of dung beetles are considered separately according to their differing abilities to tolerate many environmental variables (Lobo & Martín-Piera, 1999), the poorest assemblages can be characterized by three related features: (i) the scarcity of Aphodiidae species, (ii) the low species turnover between localities, and (iii) the high scores of the Scarabaeidae/Aphodiidae ratio which are either close to 1 or clearly biased in favour of Aphodiidae (Lobo *et al.*, 1997b; Hortal-Muñoz *et al.*, 2000). The exhaustive dung beetle inventory of the Camargue region shows a high proportion of Aphodiidae species (55%) and a Scarabaeidae/Aphodiidae ratio of 0.70. However, the assemblages observed in the coastal habitats were almost exclusively made up of Scarabaeidae (9 out of 11 species) with a 4.5 Scarabaeidae/Aphodiidae ratio. In comparison to Aphodiidae, Scarabaeidae species dominate the assemblages because they are to a greater degree habitat generalists, they possess greater dispersal abilities and they are generally more widely distributed on a geographical scale than Aphodiidae species (Lumaret & Lobo, 1996; Lobo & Martín-Piera, 1999; Hortal-Muñoz *et al.*, 2000).

Previous data (Dajoz, 1972) and the comparisons with other localities and regions suggest a decline in populations of roller dung beetles and a noticeable decrease in diversity. The dramatic decrease in species richness may be due to several factors: use of insecticide spraying to control coastal mosquito populations (especially in temporarily flooded areas) (Babinot, 1997); the treatment of cattle and horses with veterinary drugs whose residues in dung are toxic to beetles (Lumaret, 1986; Wardaugh & Mahon, 1991; Lumaret *et al.*, 1993; Herd, 1995) and/or habitat destruction as the result of urbanization and tourism. As Mediterranean coastal environments in France are rare, and as they have a high probability of being greatly altered, we recommend: (i) the monitoring of coastal insect populations in order to clarify the conservation status of these species; and (ii) that the two emblematic roller dung beetles species of the Camargue be considered for inclusion in French invertebrate protection legislation.

The comparison between the two reserves (the Camargue and Doñana) also highlights the relevance of historical and geographical factors as determinants of dung beetle diversity and the composition of assemblages in Mediterranean coastal areas. The regional species richness is similar in both regions, but changing the species composition. Only 36% of all species are shared by the French and Spanish reserves. The divergence between the Camargue and Doñana is highest for Geotrupidae (only 1 shared species out of 10), less for Aphodiidae (18 shared species out of 53), and least for Scarabaeidae (17 shared species out of 38). Most of the species present in the Camargue are widely distributed in the west Palaearctic region, compared with Doñana where 37% of the species are restricted to the southern part of the Iberian Peninsula. According to Lumaret & Lobo (1996), the highest rate of endemism in European dung beetles occurs in the Iberian Peninsula, with 39%, 19% and 11% of the west Palaearctic Geotrupidae, Scarabaeidae and Aphodiidae, respectively, being restricted to the Iberian Peninsula. This high rate of endemism is probably due to the role played by the Iberian Peninsula as a refugia and centre of vicariance during the Pleistocene ice contraction/expansion cycles (Bennett *et al.*, 1991; Hewitt, 1996; Taberlet *et al.*, 1998). This can be considered as a key determinant of the divergent composition between the

Camargue and Doñana dung beetle, in spite of the convergence of species richness observed at regional scales.

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