

SEASONAL OCCURRENCE AND HABITAT DISTRIBUTION OF TENEBRIONID BEETLES INHABITING A MEDITERRANEAN COASTAL DUNE (CIRCEO NATIONAL PARK, ITALY)

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RÉSUMÉ

La communauté de Coléoptères Ténébrionides habitant les dunes côtières d'un système protégé du littoral tyrrhénien (Parc National du Circeo, Italie centrale) a été analysée dans le but d'étudier (1) la répartition et la diversité de ces coléoptères dans trois associations végétales différentes, (2) les variations saisonnières de la composition spécifique et de la structure de la communauté. Un échantillonnage mensuel a été conduit en tamisant un volume constant de sable et de débris végétaux récolté au pied des plantes halophiles. La plupart des espèces ont montré une abondance nettement distincte dans les trois associations. La richesse et la diversité présentaient des différences mensuelles substantielles. Une diminution de la densité globale a été observée de l'association végétale la plus externe (la plus proche du bord de la mer) à la plus interne. En outre, une variation temporelle a été observée dans la dynamique des populations, avec une nette diminution de la densité durant les mois les plus chauds et les plus secs de l'été. Ces données confirment des modèles phénologiques déjà décrits pour d'autres communautés d'invertébrés du sol dans les environnements arides de la Méditerranée.

SUMMARY

The tenebrionid community inhabiting a Mediterranean dune ecosystem (Circeo National Park, central Italy) was analysed to study (1) the distribution and diversity of these beetles in three different plant associations, and (2) the seasonal changes of the community composition and structure. Monthly samplings were made by sieving a fixed volume of sand and detritus. Most species showed a different abundance in the three habitats, and substantial differences were observed in the monthly values of species richness and diversity. A decrease of the overall density was observed from the external to the innermost plant association, characterized by a higher plant cover. The community also showed clear temporal phases, with an overall decrease in winter and summer, confirming a pattern previously observed also in other soil arthropods living in Mediterranean arid environments.

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INTRODUCTION

Tenebrionid beetles (Coleoptera Tenebrionidae) are generally a major component of the fauna of arid environments such as desert and semi-desert habitat types (see Faragalla, 1999 for references). High values of tenebrionid beetle diversity and abundance have been reported for some desert areas like the Mojave desert (e. g. Thomas, 1983), NW Lybia (Fiori, 1969; Fiori & Crovetto, 1972), Saudi Arabia (Faragalla, 1998, 1999), Namib desert (e. g. Koch, 1962; Holm & Scholtz, 1980), Negev desert (Ayal & Merkl, 1994; Krasnov & Ayal, 1995; Krasnov & Shenbrot, 1997), as well as for some Mediterranean beach-dune systems (e. g. Martín Cantarino & Seva Roman, 1991; Colombini *et al.*, 1991; Fallaci *et al.* 1994, 1997).

In both desert and beach-dune ecosystems, the decomposition of detritus by bacteria and fungi is really limited by the pervading aridity. Consequently, the role of macrodetritivores like tenebrionid beetles should be significant to nutrient and energy cycling (cf. Hanrahan & Seely, 1990).

Qualitative data on habitat preference and seasonal abundance of some tenebrionid beetles of Mediterranean coastal areas were reported by Binaghi (1964), Marcuzzi (1965), Théron & Bigot (1964), Canzoneri (1966), Bonometto & Canzoneri (1970), Chelazzi *et al.* (1990), Contarini (1992) & Fattorini & Maltzeff (2001). Quantitative approaches were provided by De los Santos *et al.* (1988), Colombini *et al.* (1991, 1994), Martín Cantarino & Seva Roman (1991), Fallaci *et al.* (1994, 1997), and Fattorini & Carpaneto (2001). However, these studies dealt with tenebrionid life histories and density, or arthropod communities in general. Also, although it is known that the structure of the dunal vegetation plays an important role in influencing faunal distribution (McLachlan, 1991), the only research on the spatial and temporal organization of a tenebrionid community in the different plant associations of a dune system is one by Carpaneto & Fattorini (2001).

The present paper gives results of a study of the tenebrionid community inhabiting a Mediterranean dune ecosystem. It aims at throwing light on: (1) the distribution and diversity of tenebrionid beetles in different plant associations of the dune system; (2) the seasonal changes of community composition and structure; (3) the possible factors influencing both spatial and temporal patterns of distribution at microhabitat level.

MATERIAL AND METHODS

STUDY AREA AND SAMPLING TECHNIQUES

The study was carried out on the dune system inside the Circeo National Park and adjacent to an important Ramsar site (Lago di Caprolace, No. 71T013). This protected area is located in Central Italy (Tyrrhenian coast) and is bordered by about 25 km of coastal sand dunes (normally 10-15 m of elevation; maximum 27 m). Samplings were made on a dune site extending about 300 m in length and 50 m in width from March 1983 to February 1984.

Along a transect from the seaward slope of the most recent dune to the innermost one (where the evergreen scrub begins), the following plant associations were recognized (cf. Acosta *et al.* 2000):

(1) *Echinophoro spinosae* – *Elymetum farcti* (EE) (= *Agropyretum mediterraneum*) that is the first dune stabilizing association;

(2) *Echinophoro spinosae* – *Ammophiletum arundinaceae* (EA) (= *Ammophiletum arundinaceae*) the most characteristic association of loose substratum with great mobility of sand;

(3) *Loto cytisoidis* – *Crucianelletum maritimae* (LC) (= *Crucianelletum maritimae*) the innermost association, linked to more fixed substrata with abundant humus.

Samplings were made by sieving sand and detritus collected at the base of each different plant species occurring in each association from the surface to 10 cm depth. A total amount of 31,667 cm³ of sand and detritus was collected every month from ten well spaced tufts (choose at random) of each different plant species.

Because the number of plant species was different in each plant association (i. e., 6 in EE, 15 in EA and 13 in LC), a different volume of substrate was analysed in each one. Therefore, when the abundance of beetle species was compared among the three plant associations, data were standardized dividing values obtained in EA and LC by the volume sampled in EE.

DATA ANALYSIS

According to the overall dominance (computed as a percentage of the total number of a given species collected in the three habitats on the total tenebrionid beetles sampled), the tenebrionid beetle species were grouped as: abundant ($D \geq 5\%$), influent ($2 \leq D < 5\%$) and recedent ($D < 2\%$) (cf. Fallaci *et al.*, 1994). Also, the species were grouped according to their body size into seven dimensional classes, increasing in rank from that including the smallest species to that of the largest one. The abundance of each class (i. e. total number of specimens of the species included) was correlated with the rank by using the Spearman rank correlation test. To group species into classes of body size, we used mean values of total length obtained from the ranges reported by Fattorini & Carpaneto (2001).

As data on the life cycles of almost all species are lacking, it is difficult to distinguish between *r*- and *K*-strategists. However, as *r*-strategists are said to be generally smaller in size than *K*-strategists, we assumed that small-sized tenebrionid beetle species are *r*-strategists in comparison to large-sized species such as *E. siculus* and *P. bipunctata*. The χ^2 test was used to see if abundance of tenebrionid beetle species was significantly different between large-sized species (*E. siculus* and *P. bipunctata*) and small-sized (all the others). The null hypothesis was a uniform distribution of species abundance between the two classes (as small sized species included eight species, their total number was standardized by dividing by four).

As to the among-habitats variations in species abundance, the χ^2 test was used to see whether abundance of tenebrionid beetle species was significantly different among the three plant associations, the null hypothesis being a uniform distribution of species abundance at habitat level. For this test, we used the yearly total abundance of each species in each habitat, obtained by pooling monthly abundance values, to avoid possible biases due to temporal changes in species abundance. Pooling data should give the true overall abundance of a species in a given habitat, without respect to its phenology. A sequential Bonferroni test (Rice, 1989) was

used to adjust the significance level to the number of comparisons using the same data set.

Temporal frequencies were calculated on 12 samples considering each month as a sample. Species were thus classified as constant ($F \geq 50\%$), accessory ($25 \leq F < 50\%$), accidental ($10 \leq F < 25\%$) or sporadic ($F < 10\%$) (cf. Fallaci *et al.*, 1994).

Temporal variations in species dominance in the three plant associations were studied considering the dominance of each species in a given month as the percentage on the total number of tenebrionid beetles collected in that month.

In interpreting such results, caution should be paid because temporal variations in species abundance among habitats could be affected by species movements. At least some species of tenebrionids are known to exploit different habitats in different times (Colombini *et al.*, 1994). Therefore, monthly variations of species abundance in different plant associations could be affected by changes in the spatial distribution of the species.

Species phenologies were studied by clustering species according to their monthly abundance. We used the total monthly abundance (i. e. the abundance of a species, in a given month, in the three habitats pooled) to avoid possible biases due to temporal changes in species distribution among habitats. Pooling data by habitats should give the true phenology of a species, without respect to fluctuations of density in different habitats due to changes in their preferential exploitation. Species phenologies were correlated by the Pearson product moment correlation coefficient (r) to obtain a correlation matrix. This matrix was converted into a distance matrix ($1 - r$) and distances were clustered according the UPGMA (unweighted pair-group method using arithmetic averages) amalgamation rule.

Although species richness is generally the most relevant component of beetle diversity, due to the scarce number of species occurring in the study area and the substantial uniformity of the beetle assemblages in the three habitats, we used statistical diversity indices which include a measure of equitability. We used the Shannon diversity index (H') as a measure for community diversity and the Pielou index (J') as a measure of evenness (cf. Carpaneto & Fattorini, 2001). Monthly values of both indexes were calculated for each habitat and differences among habitats tested by a one-way ANOVA test. Note that the monthly variations of these indexes reflect the overall change in the community structure in each habitat, because both species phenology and different habitat exploitations concur to change the community structure. To assess if H' varied during the year with the same pattern in the three habitats, we correlated the monthly values obtained from EE, EA and LC, by using the Pearson coefficient. The same procedure was used to assess if J' varied during the year with the same pattern in the three habitats.

We studied also monthly variations in species richness in the three habitats. Monthly values of species richness were calculated for each habitat and differences among habitats tested by a one-way ANOVA test. To assess if species richness varied during the year with the same pattern in the three habitats, we correlated the monthly values obtained from EE, EA and LC by using the Pearson coefficient.

To study similarity between temporal tenebrionid beetle assemblages we used hierarchical clustering strategies. The complete linkage was applied to cosine similarity measures and the Ward method to Euclidean distances. We chose these procedures to make results comparable with previous studies (Krasnov & Ayal, 1995; Carpaneto & Fattorini, 2001).

In all tests, significant level was fixed at $p \leq 0.05$. Statistical analyses were performed using both STATISTICA 4.5 and NTSYS (Rohlf, 1993) software.

RESULTS

SPECIES COMPOSITION AND ABUNDANCE IN DIFFERENT HABITATS

Ten species of tenebrionid beetles were collected during this study (Table I), for a total of 7 519 specimens, of which 1 723 from EE, 3 363 from EA and 2 433 from LC. Because the actual numbers of collected specimens are affected by differences in volume of substrate (ca 2.28 m³ in EE, 5.70 m³ in EA and 4.94 m³ in LC), the ratio between specimens and volume was calculated in order to estimate the number of beetles per m³ of substrate. As a whole, the beetle density decreased from the external to the innermost plant association, the number of beetles per volume of substrate being 755.69 in EE, 589.99 in EA and 492.51 in LC ($\chi^2_{(2)} = 57.79, p < 0.001$).

With the exception of *X. pallidus* (which was represented in our samplings by only two specimens, both from EA), no differences in species composition were observed among the three habitats. Thus, the three plant associations showed almost the same overall richness (9 species in EE and LC, 10 species in EA, see Table I). Due to the scarce numbers of *X. pallidus* collected, data on this beetle were excluded from the analysis.

Looking at the yearly abundance of each species in the three different plant associations, significant differences were observed for *E. siculus* ($\chi^2_{(2)} = 8.16, p < 0.05$), *P. bipunctata* ($\chi^2_{(2)} = 9.20, p < 0.05$), *A. rufus* ($\chi^2_{(2)} = 58.49, p < 0.001$), *T. aphodioides* ($\chi^2_{(2)} = 127.89, p < 0.001$), *P. acuminata* ($\chi^2_{(2)} = 1057.72, p < 0.001$), *P. provincialis* ($\chi^2_{(2)} = 35.09, p < 0.001$), *H. pellucida* ($\chi^2_{(2)} = 9.65, p = 0.01$), and *P. normandi* ($\chi^2_{(2)} = 17.92, p = 0.001$). All χ^2 tests resisted the Bonferroni correction ($k = 9$). By contrast, no significant differences among habitats were found in the abundance of *X. pellucidus* ($\chi^2_{(2)} = 0.8, p = 0.656$). In particular, *E. siculus*, *A. rufus*, and *H. pellucida* were increasing from EE to LC, *T. aphodioides*, *P. acuminata* and *P. provincialis* showed an opposite pattern, while *P. bipunctata* and *P. normandi* were most abundant in EA (Table I).

As a whole, the most numerous (abundant) species were *A. rufus*, *P. acuminata* and *H. pellucida*. Influential species were *T. aphodioides* and *P. normandi*, while *E. siculus*, *P. bipunctata*, *P. provincialis*, *X. pallidus*, and *X. pellucidus* were recedent species. Interestingly, *P. acuminata* and *P. provincialis*, two strictly related species, showed a significant difference in their total abundance ($\chi^2_{(1)} = 1031.14, p = 0.001$).

Considering the patterns at between-habitat level, *A. rufus* was abundant in all associations; *T. aphodioides* was abundant in EE, becoming recedent in EA and LC; *P. acuminata* was abundant in EE and EA, but recedent in LC; *P. provincialis* was influential in EE, but recedent in EA and LC; *H. pellucida* was influential in EE, becoming abundant in EA and LC; *P. normandi* was recedent in EE, abundant in EA and recedent in LC.

To study the correlation between body size and abundance, species were ranked from the smallest to largest (cf. Table I) into the following body size classes:

TABLE I

Tenebrionid beetle abundance and dominance: EE = Echinophoro spinosae-Elymetum farcti; EA = Echinophoro spinosae-Ammophiletum arundinaceae; LC = Loto cytisoidis-Crucianelletum maritimae.

Species	Body length (mm)	Total number of collected specimens	Over-all dominance (%) [*]	Habitat abundance ^{**}			Habitat dominance ^{***}		
				EE	EA	LC	EE	EA	LC
<i>Erodius siculus</i> Solier, 1834	10.0-11.0	58	0.77	2	10.80	13.38	0.12	0.80	1.19
<i>Pimelia bipunctata</i> Fabricius, 1781	14.0-18.5	45	0.60	3	13.20	4.15	0.17	0.98	0.37
<i>Ammobius rufus</i> Lucas, 1849	2.5-3.8	4723	62.81	621	854.00	907.71	36.04	63.49	80.85
<i>Trachyscelis aphodioides</i> Latreille, 1809	3.0-4.0	167	2.22	101	25.60	0.92	5.86	1.90	0.08
<i>Phaleria acuminata</i> Küster, 1852	5.0-8.0	1352	17.98	824	208.80	2.77	47.82	15.52	0.25
<i>Phaleria provincialis</i> Fauvel, 1901	5.3-8.1	120	1.57	47	25.20	4.62	2.73	1.87	0.41
<i>Halammobia pellucida</i> (Herbst, 1799)	3.8-4.5	617	8.20	78	111.20	120.44	4.53	8.27	10.73
<i>Pseudoseriscius normandi</i> (Español, 1949)	4.0-5.0	325	4.32	31	74.00	50.3	1.80	5.50	4.48
<i>Xanthomus pallidus</i> (Curtis, 1830)	6.9-11.0	2	0.03	0	0.80	0.00	0.00	0.06	0.00
<i>Xanthomus pellucidus</i> (Mulsant, 1856)	6.0-9.0	110	1.46	16	21.60	18.46	0.93	1.61	1.64

* Overall dominance = species abundance/ total number of tenebrionid beetles (7519) x 100

** Habitat abundance = number of specimens per standard volume of substrate (2 280 024 cm³)

*** Habitat dominance = species abundance/number of tenebrionid beetles (1 723 in EE, 3 363 in EA, 2 433 in LC) x 100.

(1) *A. rufus* and *T. aphodioides*, (2) *H. pellucida*, (3) *P. normandi*, (4) *P. acuminata* and *P. provincialis*, (5) *X. pallidus* and *X. pellucidus*, (6) *E. siculus*, (7) *P. bipunctata*. Species abundance values were significantly correlated to the rank of the body size classes, decreasing from the smallest to the largest species ($r_s = -0.89$, $p < 0.01$).

As a whole, a significant difference in abundance was observed between large-sized (*E. siculus* and *P. bipunctata*) and small-sized species (all the others) ($\chi^2_{(1)} = 1566.68$, $p < 0.001$).

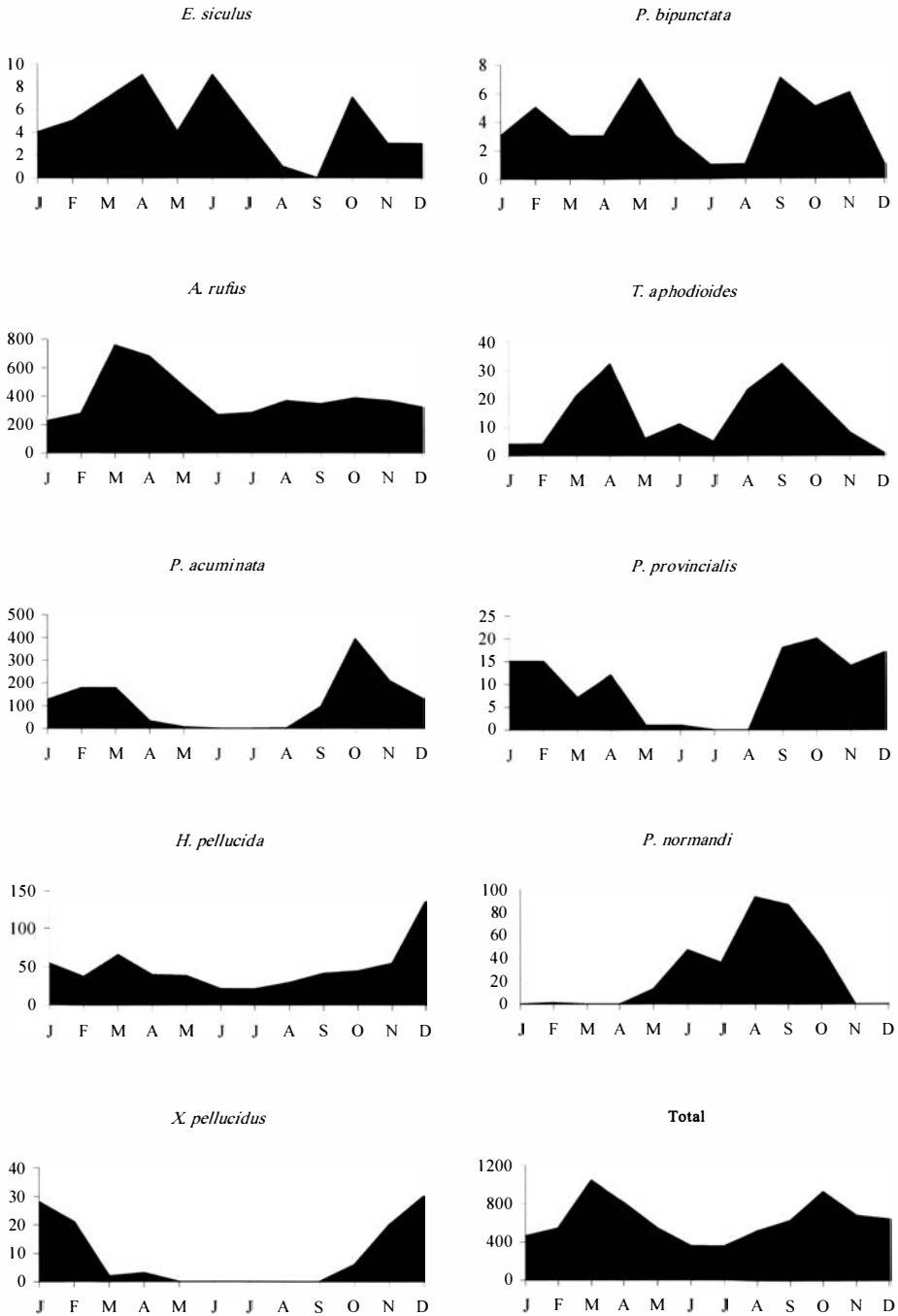


Figure 1. — Phenology of tenebrionid beetles in the study area.

SEASONAL CHANGES IN SPECIES COMPOSITION

With the exception of *X. pallidus* (a species which appeared to be accidental in the sampling), all species occurred in the study area during almost the whole year.

As to the species phenology (Fig. 1), *H. pellucida*, *P. acuminata*, *P. provincialis* and *X. pellucidus* showed similar phenological patterns characterized by drops from May to July. Even if represented by a reduced number of specimens, also *P. bipunctata* showed a substantial summer decrease. By contrast, *P. normandi* is a temporal specialist with a typically summer phenology. Finally, *A. rufus*, the most abundant species, appeared to be relatively abundant through the year, increasing in spring, while *E. siculus* and *T. aphodioides* showed a rather irregular pattern. Cluster analysis of species phenologies strongly supports such groupings (Fig. 2). As a whole, the tenebrionid community seems to drop in summer (Fig. 1).

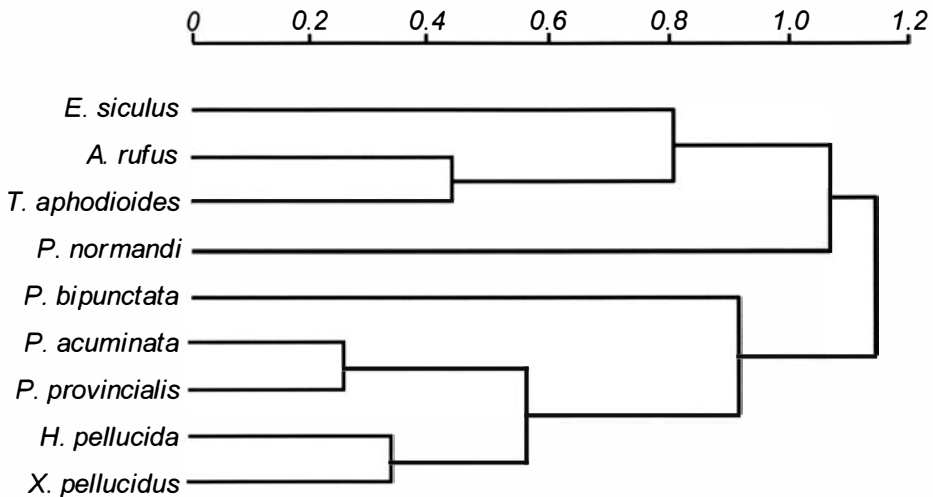


Figure 2. — Dendrogram yielded by hierarchical cluster analysis of monthly phenologies of tenebrionid beetles in the study area. Phenologies were correlated by the Pearson coefficient (r). A UPGMA amalgamation rule was applied to a distance matrix ($r - 1$).

Looking at the dominance of each species in the three habitats during the year (Fig. 3), we can note that: (1) *A. rufus* is an important element through the year in each habitat; (2) *P. acuminata* is an important element in autumn and winter in EE and, with lower proportion, in EA; (3) *P. normandi* is an important summer element, especially in EA and LC.

Although the three habitats shared the same tenebrionid species over the year, monthly variations in species richness were detected in each habitat. Monthly variations in species richness showed a significant correlation only between EA and LC ($r = 0.7136$, $p < 0.01$). Richness varied from 3 to 6 species (mean value \pm S.D.: 5.17 ± 1.03) in EE, from 4 to 9 (6.92 ± 1.51) in EA, and from 4 to 7 (5.17 ± 1.03) in LC. A comparison among monthly variations in the three habitats by ANOVA was significant ($F_{(2,33)} = 8.38$, $p < 0.01$).

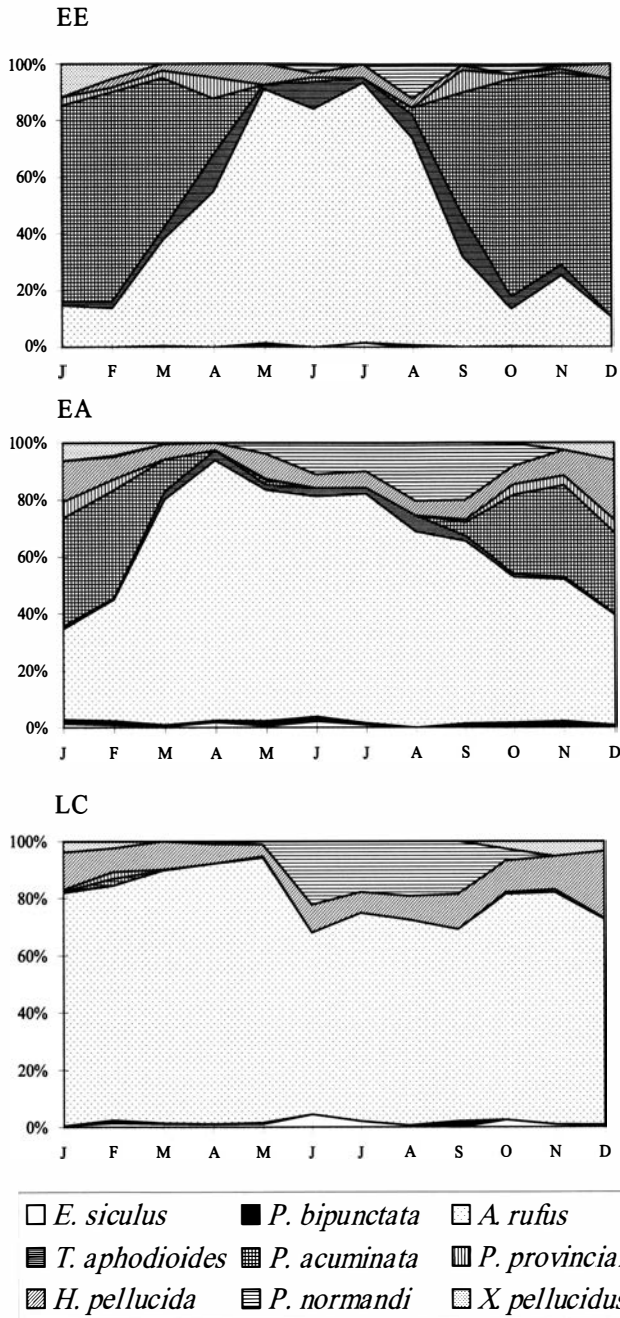


Figure 3. — Relative abundance of tenebrionid beetles in the three plant associations. EE = *Echinophoro spinosae* — *Elymetum farcti*; EA = *Echinophoro spinosae*-*Ammophiletum arundinaceae*; LC = *Loto cytisoidis* — *Crucianelletum maritimae*.

Both H' and J' values varied without regularity along the year. For both H' and J' no significant correlations were found between the three habitats. H' varied from 0.36 to 1.30 (mean value \pm S.D.: 0.83 ± 0.30) in EE, from 0.40 to 1.52 (1.03 ± 0.35) in EA, and from 0.36 to 0.99 (0.69 ± 0.21) in LC. J' varied from 0.26 to 0.78 (0.51 ± 0.15) in EE, from 0.25 to 0.73 (0.53 ± 0.15) in EA, and from 0.20 to 0.71 (0.44 ± 0.17) in LC. A comparison among monthly variations in the three habitats by ANOVA test was significant for H' ($F_{(2,33)} = 4.22, p < 0.05$), but not for J' ($F_{(2,33)} = 1.23, p = 0.306$).

Cluster analysis of temporal assemblages of tenebrionid beetles showed a very clear correspondence between community's dynamics and seasons (Fig. 4a,b).

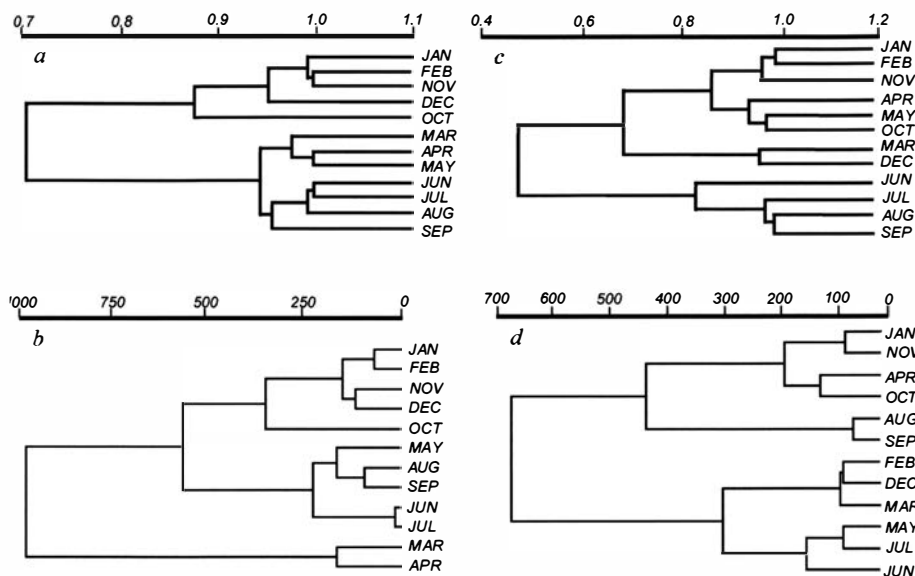


Figure 4. — Dendrograms yielded by hierarchical cluster analysis of monthly assemblages of tenebrionid beetles in the study area (a, b) and at Castelporziano, another Tyrrhenian area (c, d): (a, c) cosine measure and complete linkage, (b, d) Euclidean distances and Ward's method.

For comparison purposes, the same clustering strategies were applied to data sets from Castelporziano (Fig. 4c,d), another Tyrrhenian site, with similar ecological conditions, studied by Carpaneto & Fattorini (2001).

DISCUSSION

The differences in the tenebrionid beetle spatial assemblages between the three dune habitats studied at Circeo, as well as their monthly variations, involve important changes in relative abundance of the species. The overall species richness was almost identical in all habitats, but significant temporal variations were observed in the mean value of species richness among habitats. However, as observed in other studies (cf. Thomas, 1983; Martín Cantarino & Seva Roman, 1991; and references

therein), the ecological optima of the studied species do not segregate into discrete habitat and temporal partitions in any obvious way. On the contrary, substantial overlaps in phenology and habitat distribution were observed. However, habitat differences seem to influence beetle abundance, while phenologies are probably moulded by climatic changes.

As a whole, species abundance was correlated with body size, the smallest beetles being the most abundant. These results fit a pattern described by Ayal & Merkl (1994) in the tenebrionid beetle communities in the Negev desert, where the most abundant species were all relatively small. As the small-sized species were significantly more abundant than the large-sized species (i. e. *E. siculus* and *P. bipunctata*), we believe that the latter, probably operating under a *K* mode of selection, actually form less dense populations, compared with all other tenebrionid beetles collected in the study area. Data for both *E. siculus* and *P. bipunctata* population sizes obtained by Fallaci *et al.* (1997) support the idea that these species have relatively small populations.

With the exception of *X. pellucidus*, all species appeared to be distributed with significant differences over the three habitats. In particular, *P. normandi* appeared to be linked to the innermost part of the dune, whereas *P. acuminata* and *P. provincialis* showed a clear decrease from EE to LC. According to Tongiorgi (1969) and Colombini *et al.* (1994), *P. provincialis* seems to be a strictly halophilic species decreasing from the foreshore to the dunes, at least in Tuscany region. Our data are consistent with these findings, also suggesting an halophilic preference for *P. acuminata*. As observed by Colombini *et al.* (1994) for *P. provincialis* and *P. bimaculata*, the overlapping habitat distribution of *P. acuminata* and *P. provincialis* suggests that there is no clear habitat subdivision between these two species. The latter is an extremely rare phenomenon in coastal dune system (McLachlan, 1991). However, *P. provincialis* is a recedent species in the study area, quite less abundant than *P. acuminata*, perhaps as a result of a possible competition between these two strictly related species.

According to McLachlan (1991), proceeding from the beach landwards, there is an increase in insect species diversity and abundance. By contrast, the tenebrionid beetle assemblages within the study area showed opposite patterns, in that density was decreasing from EE to LC. Carpaneto & Fattorini (2001) observed the same pattern (i. e. tenebrionid density decreasing from EE to LC) at Castelporziano. This pattern can be related to the peculiar xerophilic and termophilic adaptations to arid environments of the tenebrionid beetle assemblages, which make these detritivorous insects more favoured in exploiting sand-dunes habitats than other species. The peculiar microclimate of the seaward margin of the dune, which represents important constraints for most insects, does not act so negatively on tenebrionid species that are well adapted to such conditions (Carpaneto & Fattorini, 2001). Also, in a well preserved (i. e. not cleared) coastal environment there is an important detritus input from the sea, that mostly regards the seaward margin of the dunes (i. e. EE and EA), in addition to the detritus produced by plants living here. According to McLachlan (1991), on beaches receiving large marine inputs even the dune chains may be strongly dependent on these subsidies with much of the fauna located near the dune/beach interface.

Even if all habitats shared the same species, monthly values of species richness and diversity (and possibly also of evenness) seem to be enhanced in EA. Because of its intermediate location, EA acts as an ecotone. Thus, EA probably has not a preferential character for almost any species, being suitable for both typically beach-

dwelling species (such as *Phaleria* spp.) and typically dune-dwelling species (such as *E. siculus* and *P. bipunctata*), allowing for reduced dominances.

As a whole, in each habitat, the temporal structure of the tenebrionid beetle assemblages showed substantial monthly changes in the dominance of the different species. Also, in accordance with other studies (e. g. Krasnov & Ayal, 1995), clear temporal phases can be observed in the monthly assemblages. The distinctly separate position of March and April obtained by applying the Ward method to Euclidean distances is probably due to their transitional character between winter and summer. In contrast with these results, less clear temporal assemblages can be observed in the tenebrionid community of Castelporziano (Fig. 4). Carpaneto & Fattorini (2001) hypothesized that the irregularity observed at Castelporziano could be due to the ecological instability of sand dunes and human disturbance. Results obtained at Circeo suggest that the irregularity at Castelporziano is probably more dependent on the moderate human pressure in this site during summer, which represents a potential disturbance for the seasonal cycle of the community, rather than on ecological factors.

As with the species phenologies, *P. normandi* is the only species which reaches its highest density in summer, being a partly ecological vicariant of the other dominant tenebrionid beetles. However, even *P. normandi*, which is a temporal specialist, has its adult activity period within the phenologies of the other species. As a rule, the long activity period of most species and their temporal coincidence suggest that seasonal partitioning does not play a major role in reducing species competition.

At Circeo most species occur as adults also during winter, probably as over-wintering individuals sheltered in the soil, and which could have a “two-year life cycle” such as that observed for large sized tenebrionids by De los Santos *et al.* (1988). However, most of the species show low densities in winter months. Also, all the most abundant species but *P. normandi* showed phenologies with summer drops, confirming a general pattern of ground arthropod populations in southern Mediterranean coastal areas (cf. Dajoz, 1987; Hornung & Warburg, 1995). Thus a general pattern can be outlined for the tenebrionid beetles at Circeo, characterized by winter and summer drops followed by autumn and spring increases. A similar pattern was observed in Saudi Arabia, where summer and winter tenebrionid disappearance was correlated to non-optimal or even intolerable temperatures (Aldryhim *et al.*, 1992).

Finally, in contrast with the phenological patterns observed at Burano, in Tuscany (Colombini *et al.*, 1994; Fallaci *et al.*, 1997), at Circeo, as well as at Castelporziano (Carpaneto & Fattorini, 2001), all species but *P. normandi* do not have summer increases, but when seasonal differences are clearly recognizable they consist in summer decreases. Indeed, the phenological patterns found at Circeo showed patterns similar to that recorded in Tuscany, but with the maximum peak of density apparently shifted towards autumn. Even if the differences between the sampling methods used by us (sieving) and by Chelazzi *et al.* (1990) (trapping) could be involved, these contrasting results are more likely related to different rainfall patterns. At Burano (Chelazzi *et al.*, 1990) rainfalls occur in June and July, favouring a summer increase in beetle abundance. By contrast, at Circeo, heavy rainfalls occur in later summer (Pezzotta, 1998) allowing a population increase after August, as also observed at Castelporziano (Carpaneto & Fattorini, 2001). As postulated for two asidine tenebrionid beetles whose activity period corresponded with the late summer rainfall (Thomas, 1983), autumnal increases in species abundance can be related to the late summer rainfalls, which could be critical for beetle reproduction and for survival of immature stages.

To conclude, in contrast with the general insect pattern outlined by McLachlan (1991), the tenebrionid beetle species showed a decrease in their abundance from the seaward to the landward margin of the dune, probably as a consequence of their ability to exploit habitats (i. e. plant associations occurring on the external side of the dune) which are less suitable for other insects. Also, while species diversity generally increases from the beach landwards, we observed high mean values of species richness and diversity in the plant association which occupies the central part of the dune. This is probably a consequence of its transitional character, making this plant association a suitable habitat for both species typically linked to the beach and those more associated with inland plant associations. Finally, as observed for other terrestrial arthropods in southern Mediterranean coastal areas (cf. Dajoz, 1987; Hornung & Warburg, 1995), all the most abundant species but *P. normandi* showed phenological patterns with summer drops, probably as a consequence of the high temperature in summer.

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