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Flightlessness in psammophilous beetles inhabiting a Mediterranean coastal area: ecological and biogeographical implications

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SUMMARY

Many psammophilous beetles are known to be wingless ground dwellers, and flightlessness has been frequently regarded as an adaptation to arid environments. Also, as flightlessness reduces dispersal ability, flightless species should have reduced ranges compared with those of winged species. The aim of this work was to study (1) the incidence of flightlessness in the psammophilous beetles living in a Mediterranean beach-dune system, and (2) possible relationships between distribution patterns and wing conditions. The study was based on the beetle fauna living on the beach-dune system of the Circeo National Park (Central Italy, Tyrrhenian coast). To obtain a complete faunal inventory of the true psammophilic beetles, monthly samplings were performed by sieving a fixed volume of sand and detritus. A total of 26 strictly psammophilous species, belonging to 10 beetle families were recorded. As a whole, 10 species were apterous, 5 brachypterous and 11 macropterous. If apterous and brachypterous species are computed together as flightless species, we found a total of 15 flightless species (57.69%) versus 11 macropterous species (42.31%). In accordance with the geographical location of the study area and the thermophilic preferences of many species, most of the species have distribution patterns restricted to Mediterranean or South European areas, only two being more widely distributed. As to the size of their ranges, 12 (46.15%) species showed restricted distributions (i.e. types of distribution restricted to the western or the eastern sector of the Mediterranean basin), while 14 (53.85%) were widely distributed. As a whole, a relationship can be observed between flightlessness and species ranges. Most (83.33%) of the species with reduced ranges are flightless. By contrast, flightless species represent 35.71% of the widely distributed species.

A number of factors and circumstances can be evoked to explain the occurrence of flightlessness in the study community. Dune habitats are distributed so that a ground dwelling insect can move from one patch to another by walking and burrowing, a condition that can favour flightlessness. As coastal dunes have scarce trophic sources, loss of flight could allow to conserve energy that can be allocated to other functions. Due to their high winds, coastal dunes require a great amount of energy for flight. Shoreline strands are clearly isolated habitats, with unfriendly and isolating habitats on each side, favouring non-dispersing individuals. Finally, a high incidence of flightlessness in some beetles can be due to their burrowing lifestyle and detritivorous habits.

As a whole, flightless species show more restricted ranges compared with winged species. Thus, even if many littoral beetles are known to be capable of swift movement on the ground, flightlessness probably plays an important role in determining a reduced dispersal ability, which, in turn, affects species distributions.

INTRODUCTION

Psammophilous beetles are a prominent component of desert and semi-desert habitats, because of their high biomass and richness, as observed in the Mojave desert (e.g. Thomas, 1983), Namib desert (e.g. Koch, 1962; Holm and Scholtz, 1980), Negev desert (Ayal and Merkl, 1994; Krasnov and Ayal, 1995; Krasnov and Shenbrot, 1997) and NW Lybia (Fiori, 1969; Fiori and Crovetto, 1972).

Most psammophilous beetles are also an important component of soil faunas in Mediterranean beach-dune systems (e.g. Marcuzzi, 1965; Martin Cantarino and Seva Roman, 1991; Colombini et al., 1991; Fallaci et al. 1994, 1997). Coastal dunes are typically hot and dry habitats, and many beetles of such ecosystems exhibit particular adaptations (cf. Colombini et al., 1994 and references therein). For instance, tenebrionids living in arid habitats like deserts and coastal dunes change their activity and zonation to suit climatic conditions on both seasonal and daily basis (e.g. Colombini et al., 1994; Fallaci et al., 1997; and references therein).

As water is an important limiting factor in arid environments, beetles that live there have a number of physiological adaptations to obtain and maintain water (see Marcuzzi, 1960a, 1960b; Nicolson, 1990 for reviews). Finally, body size, body convexity, epicuticular wax bloom, colouring, integumental sculpture, presence of subelytral cavity, as well as the type of elytral interlocking mechanism represent well known morphological adaptations in such insects (Marcuzzi, 1960a, 1960b; Fiori, 1977; McClain and Gerneke, 1990; Nicolson, 1990; Heinrich, 1993; Colombini et al., 1994; Krasnov et al., 1996).

Psammophilous insects, such as many tenebrionids and carabids (e.g. Roff, 1990), are known to be wingless ground dwellers, and flightlessness has been frequently regarded as an adaptation to arid environments (cf. Marcuzzi, 1960b).

As flight plays an obviously important role in insect dispersal, and soil-dwelling tenebrionids are generally flightless, flightlessness could explain the high rates of endemism frequently observed in these beetles (cf. Fattorini, 2000). More in general, as flightlessness reduces dispersal ability, flightless species should have reduced ranges compared with those of winged species.

The aim of this work was to study: (1) the incidence of flightlessness in the psammophilous beetles living in a Mediterranean beach-dune system, and (2) possible relationships between distribution patterns and wing conditions.

MATERIALS AND METHODS

The present study was based on the beetle fauna living on the beach-dune system of the Circeo National Park. 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 in a

dune site located in front of an important Ramsar site (No. 71T013: Lagoon of Caprolace) and extending about 300 m in length and 50 m in width (Fig. 1).

To obtain a complete faunal inventory of the true psammophilic beetles, monthly samplings were performed from March 1983 to February 1984 by sieving a fixed volume of sand and detritus. Samplings were made along a transect from the seaward slope of the most recent dune to the innermost one (where the evergreen scrub begins). Along this transect, the following phytosociological associations are recognisable (cf. Acosta et al., 2000): (1) *Echinophoro spinosae-Elymetum farcti* (the first dune stabilising association); (2) *Echinophoro spinosae-Ammophiletum arundinaceae* (the most characteristic association of loose substratum with great mobility of sand); and (3) *Loto cytisoidis-Crucianelletum maritimae* (the innermost association, linked to more fixed substrata with abundant humus). In each plant association, 10 separate sampling sites were chosen at random, and within each site 3,166.7 cm³ of sand and detritus (corresponding to the volume of the sieve employed) were monthly collected under each plant species.

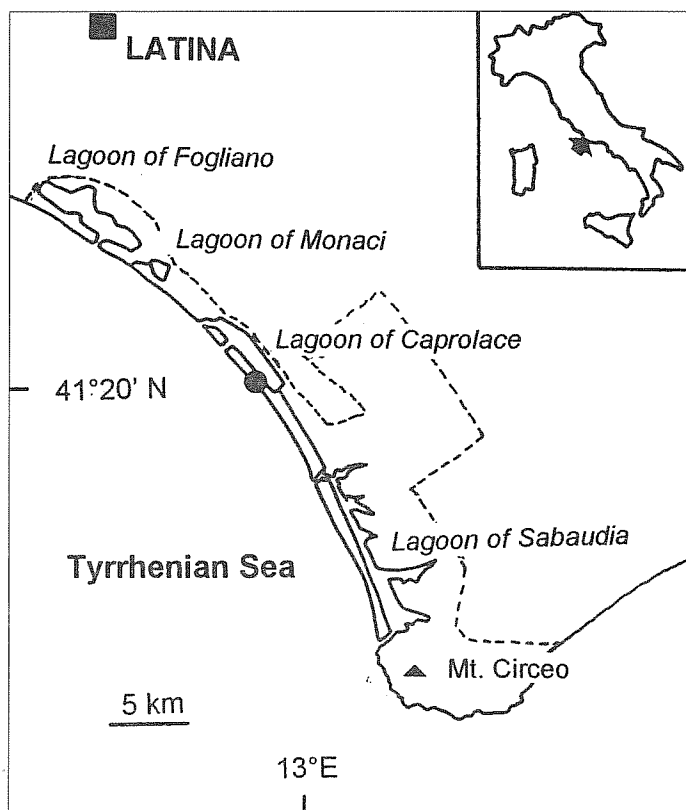


Fig. 1 - Study area. Location of the sampling site is denoted by a dot

Specimens of Scarabaeoidea and Tenebrionidae were directly identified by the authors; those of other families by other specialists (see Acknowledgements).

Analysis of wing conditions was restricted to true psammophilous species. Wing condition was studied by examining several specimens of both sexes for each species, which were classified into the following categories: (1) apterous species (species with wings completely absent and elytrae coapted); (2) brachypterous (wings at most reaching the elytral apex, or the second visible tergite for the Staphylinidae); (3) macropterous (species with well developed wings).

Based on their general distribution, species were grouped into general patterns according to the types of distribution (chorotypes) proposed by Vigna Taglianti et al. (1999).

RESULTS

A total of 26 strictly psammophilous species, belonging to 10 families (Carabidae, Histeridae, Staphylinidae, Aphodidae, Scarabaeidae, Rutelidae, Tenebrionidae, Anthicidae, Chrysomelidae and Curculionidae) were recorded. For each species, taxonomic identification, distribution pattern and wing condition are reported in Tab. I. No polymorphic species were found. As a whole, 10 species were apterous, 5 brachypterous and 11 macropterous. If apterous and brachypterous species are computed together as flightless species, we found a total of 15 flightless species (57.69%) versus 11 macropterous species (42.31%).

Tab. I - Psammophilous species recorded at the Circeo National Park

	Distribution type	Wing condition
CARABIDAE		
<i>Scarites buparius</i> Forster, 1771	W-Mediterranean	apterous
HISTERIDAE		
<i>Hypocaccus rugifrons</i> (Paykull, 1798)	Sibero-European	macropterous
<i>Baeckmanniolus dimidiatus</i> (Illiger, 1807)	Europeo-Mediterranean	macropterous
<i>Xenonychus tridens</i> (Duval, 1852)	W-Mediterranean	macropterous
STAPHYLINIDAE		
<i>Phytosus balticus</i> Kraatz, 1859	W-Mediterranean	brachypterous
<i>Phytosus nigriventris</i> (Chevrolat, 1843)	W-Mediterranean	brachypterous
APHODIIDAE		
<i>Psammodioides basalis</i> (Mulsan and, Rey, 1871)	Mediterranean	macropterous
<i>Psammodioides pierottii</i> Pittino, 1979	S-European	macropterous
<i>Brindalus porcicollis</i> (Illiger, 1803)	Mediterranean	apterous
SCARABAEIDAE		
<i>Scarabaeus semipunctatus</i> Fabricius, 1792	Mediterranean	macropterous
RUTELIDAE		
<i>Anomala devota</i> Rossi, 1790	W-Mediterranean	macropterous

TENEBRIONIDAE

<i>Erodium siculus</i> Solier, 1834	E-Mediterranean	apterous
<i>Pimelia bipunctata</i> Fabricius, 1781	W-Mediterranean	apterous
<i>Ammobius rufus</i> Lucas, 1849	Mediterranean	apterous
<i>Trachyscelis aphodioides</i> Latreille 1809	Mediterranean	macropterous
<i>Phaleria acuminata</i> Küster, 1852	Mediterranean	brachypterous
<i>Phaleria provincialis</i> Fauvel, 1901	W-Mediterranean	brachypterous
<i>Halammobia pellucida</i> (Herbst, 1799)	W-Mediterranean	apterous
<i>Pseudoseriscius normandi</i> (Español, 1949)	W-Mediterranean	brachypterous
<i>Xanthomus pallidus</i> (Curtis, 1830)	W-Mediterranean	apterous
<i>Xanthomus pellucidus</i> (Mulsant, 1856)	Mediterranean	apterous

ANTHICIDAE

<i>Anthicus fenestratus</i> (Schmidt, 1842)	Mediterranean	macropterous
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CHRYSOMELIDAE

<i>Psylliodes marcidus</i> (Illiger, 1807)	Mediterranean	macropterous
<i>Psylliodes puncticollis</i> Rosenhauer, 1856	Mediterranean	macropterous

CURCULIONIDAE

<i>Otiorhynchus juvenicus</i> Gyllenhal, 1834	W-Mediterranean	apterous
<i>Leptolepurus meridionalis</i> (Jacquelin du Val, 1854)	Mediterranean	apterous

Most of the species have distribution patterns restricted to Mediterranean or South European areas (Fig. 2), only two (*Psammodytes pierottii* and *Hypocaccus rugifrons*) being more widely distributed.

As to the size of their ranges, 12 (46.15%) species showed restricted distributions (i.e., types of distribution restricted to the western or the eastern sector of the Mediterranean basin), while 14 (53.85%) were widely distributed.

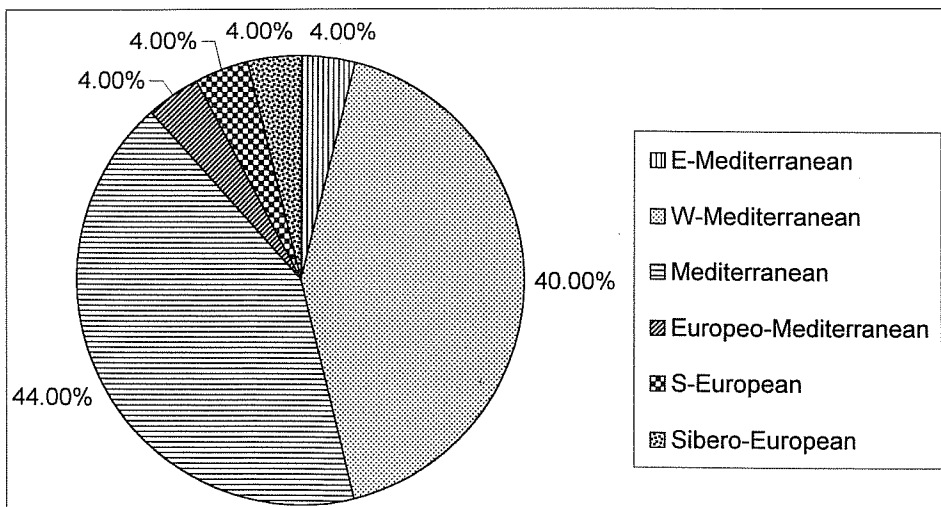


Fig. 2 - Chorological spectrum of the psammophilous beetle fauna recorded at the Circeo National Park

As a whole, a relationship can be observed between flightlessness and species ranges. Most (83.33%) of the species with reduced ranges (i.e., W- and E-Mediterranean species) are flightless. By contrast, flightless species represent 35.71% of the widely distributed species.

For many species, a possible subspecific differentiation has been proposed by various authors. However, most of the populations recognised as distinct subspecies show a very low degree of morphological divergence and their taxonomic value is questionable. In fact, only *Pseudoseriscius normandi* includes two well differentiated allopatric populations that could be actually two distinct species or subspecies.

DISCUSSION

In accordance with the geographical location of the study area, most species have ranges that fall within the Mediterranean area. This fact fits also with the thermophilic preference shown by many psammophilous species (Fallaci et al., 1997). Many beetles collected in the study area are flightless. In fact, aptery commonly occurs among tenebrionids (Fattorini, 2000), and, since tenebrionids are the most important group in the beetle community studied here, aptery cannot be exclusively regarded as an adaptation to arid environments. For example, life under bark of trees may favour modifications that will lead to loss of wings, and flightlessness actually occurs in many subcortical tenebrionid species (e.g. several Helopini). Likewise, life at high altitude may favour flightlessness, as shown by some Tenebrionidae like Asidini (a tribe with several montane species) and Geotrupidae of the genus *Thorectes*. However, a high proportion of flightless species in the beetle community of the study area could have been positively selected by the environmental conditions of the beach dune system.

In particular, the tenebrionid beetles recorded in the study area clearly possess a number of adaptations to the life in arid environments.

The nocturnal species (*Halammobia pellucida*, *Phaleria acuminata*, *P. provincialis*, *Xanthomus pallidus*, *X. pellucidus*) found on the dunes studied here exhibit a number of morphological characteristics, such as pale colouring, small size, lesser convexity, and lack of a longitudinal coaptation between the elytra, that are regarded as adaptations to nocturnal activity, when the risk of dehydration is low (cf. Colombini et al., 1994; pers. obs.). By contrast, the diurnal species *Erodius siculus* and *Pimelia bipunctata* have various morphological characteristics, such as dark colouring, larger size, greater elytral convexity, coapted elytra, thicker chitin, which are probably adaptations to avoid dehydration (cf. Colombini et al., 1994; pers. obs.). In addition, let us remark that all these species, both diurnal and nocturnal, have a subelytral cavity, particularly evident in the genera *Halammobia* and *Xanthomus*, which is also regarded as an adaptation to arid and hot habitats (cf. Colombini et al., 1994).

Generally speaking, flightlessness has evolved because there is a substantial cost to fly, as proved by the high mass of muscles required for flight and the negative correlation between fecundity and flight ability in females of wing dimorphic insects (Roff, 1984, 1986). A number of factors and circumstances can be evoked to explain flightlessness: habitat stability, habitat uniformity, habitat isolation and species lifestyles.

There may be circumstances in which adaptations for achieving dispersal retain great importance even in uniform and predictable environments (Hamilton and May, 1977). However, as habitat stability increases, selection will probably favour an increasing proportion of nondispersers, since energy can be immediately channelled into reproduction (Roff, 1986). Thus, in an environment that allows a population to persist for a long time, flightlessness should dominate. For example, in Homoptera and Hemiptera Gerridae the degree of brachyptery is correlated with the stability of the habitats, while flightless orthopterans definitively seem to occur in what appears to be a predictable and stable environment (Roff, 1986, 1990). On the other hand, wingless beetles, due to their low mobility, would undergo extinction during changes in the environment, and therefore they are good indicators of stable habitats (Brühl, 1997). Habitat stability is therefore generally acknowledged as the most important explanation for loss of flight in insects, although isolation and energetic costs might interrelate (Wagner and Liebherr, 1992).

Are coastal dunes systems actually stable and predictable ecosystems? As observed by McLachlan (1991), compared with desert dunes, coastal dunes are not marked by pulses, although wrack inputs from the sea may be erratic following storms, and rainfall may be seasonal; rather, they have more constant climates and organic inputs, and often exhibit clear succession in their vegetation.

In addition, coastal dunes are invariably long, narrow strips, where physical, chemical and vegetational variations occur only along a gradient perpendicular to the shore (McLachlan, 1991). Therefore, dune habitats are distributed so that a ground dwelling insect can move from one patch to another by walking and burrowing, a condition that can favour flightlessness (cf. Roff, 1986).

As observed for tiger beetles of saline habitats (Kamoun and Hogenhout, 1996), flight is a waste of valuable energy and even a possible hazard to reproducing, since natural habitats are isolated and food is scarce. It is important to remember that coastal dunes are ecosystems with scarce trophic sources and vegetation cover, height and diversity increasing landwards (cf. McLachlan, 1991). In such conditions of scarce energy, loss of flight could allow to conserve energy that can be allocated to other functions, such as into eggs or mate search.

Also, it is known that flightlessness is often encountered where flight has higher energetic costs (Brühl, 1997; Roff, 1990). Due to their high winds, coastal dunes require a great amount of energy for flight.

Dispersal may also be at risk in isolated habitats, because the dispersers may fail to locate a favourable habitat (Roff, 1986). Therefore, it is thought that not being able to fly keeps flightless insects from being swept to non-hospitable habitats. Are coastal dunes isolated habitats? Strand habitats like the shorelines of lakes, rivers, and oceans, and around islands, has often been associated with wing reduction and loss (e.g. Wagner and Liebherr, 1992). Coastal dunes are narrow strips hugging the coast, with distinct boundaries determined by the sea- and landward limits of eolian sand transport (McLachlan, 1991). Shoreline strands are clearly isolated habitats, with unfriendly and isolating habitats on each side. Thus, as flyers could reach non-hospitable inland habitats (e.g. evergreen scrub or forest), or can be blown over the sea, they should experience higher mortality than non-dispersing individuals.

A high incidence of flightlessness in some beetles can be due to their burrowing lifestyle and detritivorous habits. Fossorial life combines well with flightlessness, as well as the spatial distribution of detritus deposits, and their persistent nature, probably reduces the need to fly in detritivores (Holm and Scholtz, 1979). Fossorial life is common in sand dwelling insects, as well as detritivorous feeding habits are strongly selected in these habitats with scarce vegetation cover. Unfortunately, there is a certain lack of information on the feeding habits and lifestyle of the species recorded at Circeo, but data available on various species (Colombini et al., 1994; Fallaci, 1997; pers. obs.) strongly suggest that most of the species are fossorial detritivores. Finally, loss of wings allows the presence of a subelytral cavity, which is a common beetle adaptation to the life in arid environment (cf. Colombini et al., 1994).

From an historical point of view, coastal dune systems are geologically young, a consequence of changing climates and sea levels. It should be also remembered that during the Pleistocene the beach-dune ecosystems have variously changed their extension and geographic location, but such habitats did not substantially changed their environmental conditions. In other words, as postulated by La Greca (1975), coastal areas represented a stable habitat also during Pleistocene climatic changes. Therefore, the fauna of present dunes can be actually derived from faunas of ancient dunes of different geographic location. Thus, the stability of dune habitats could be confirmed even from a geological time perspective.

It is also generally assumed that in flightless insects long-distance dispersal can be discounted, and therefore apterous beetles should be very conservative indicators of historical events.

Present dispersal across the sea by drifting vehicles can not be excluded in explaining the wide distribution of some psammophilous apterous beetles. For instance, passive transport on the water by rafts seems to be occurring in various beetles between continents and also between mainland and islands (Brühl, 1997; Howden, 1977). However, as most widely distributed species occur in some areas

with relictual populations, their disjunct distributions are probably a result of past vicariance events. The following examples may be mentioned: *Pseudoseriscius normandi* (Leo, 1982) occurs in coastal areas of both Tyrrhenian Italy and Tunisia; *Phaleria provincialis* occurs on the North West Mediterranean shores on one side, and on Cyprus on the other side (Grimm, 1991); *Halammobia pellucida*, widely distributed along the Tyrrhenian coasts, also occurs on Zakynthos and in Peloponnese (Moragues, 1988; Whitehead, 1997; Fattorini, 2002a); *Xanthomus pellucidus* and *Brindalus porcicollis* are widely distributed in the West Mediterranean basin, occurring with scattered populations in the East Mediterranean (Canzoneri, 1959; Whitehead, 1997). Such disjunct distributions, which involve a major area and one or few isolated populations, are probably due to vicariance events which have broken previously continuous ranges reached through dispersal on the ground before the final structuring of the Mediterranean sea.

Finally, as can be expected, flightless species show more restricted ranges compared with winged species.

Thus, even if many littoral beetles (e.g. *Erodium siculus*, *Phaleria* spp., *Halammobia pellucida*, and *Xanthomus* spp.) are known to be capable of swift movement on the ground, also covering relatively large distances in short times (cf. Colombini et al., 1994), aptery probably plays an important role in determining a reduced dispersal ability, which, in turn, affects species distributions.

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