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Siagona europaea Dejean and *Poecilus* (*Metapedius*) *pantanellii* A. Fiori (Coleoptera: Carabidae): two clay-soil dwelling species with different uses of the space

F. TALARICO[1], F. CAVALIERE[2], A. GIGLIO[2], A. MAZZEI[1], & P. BRANDMAYR*[2]

[1]*Natural History Museum and Botanical Garden, University of Calabria, Cosenza, Italy, and* [2]*Department of Biology, Ecology and Earth Science (DiBEST), University of Calabria, Cosenza, Italy*

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Abstract
Siagona europaea and *Poecilus pantanellii* are two carabid beetles strictly bound to clay soils typical of the Italian Apennines. The first exhibits a very flat body whereas the other has more "normal" proportions, suggesting a very different use of space. We tested the use of space of both species using three sets of live pitfall traps put in place at different depths in the clay soil of a Mediterranean *Hedysarum* pasture. *Poecilus pantanellii* is a very early spring breeder and more than 90% of its individuals show epigean locomotory activity. *Siagona europaea*'s activity begins later, when the clay fissures become larger and deeper, and in the months of June and July about 80% of its population lives in the subterranean soil crevices. Morphometric measurements support these space use strategies: *P. pantanellii* has a wider antenna/eye angle and shorter antennae, indicating a possible visual component in prey recognition, as well as a thicker body and robust trochanters linked to "wedge pushing"; whereas *S. europaea* has longer antennae and a smaller antenna/eye angle suitable for olfactory-tactile prey recognition, and also has an extremely flat body and small trochanters. In the summer individuals climb up and down in the crevice system of clays searching for their specialised prey (worker ants exploring the space around their ant nests).

Keywords: *Morphometric measurements, habitus, carabids, habitat choice*

Introduction

In carabid beetles, there is a direct correlation between body form and habits (Forsythe 1991), related with their different lifestyles. Carabids also differ in many physiological and behavioural characteristics that reflect specific habitat demands (Thiele 1977; Den Boer 1986). Ground beetles that live in restricting or confined habitats, such as in fissures in the ground, have a tendency to be narrower in width and shallower in depth, with a prothorax similar in width to the hind body. It has been suggested that this body form would minimise friction by causing less obstruction when moving through confined spaces (Forsythe 1987). At first glance, most ground beetles, even of varying sizes, seem to have a similar body shape, but there are species-specific or taxon-linked differences and morphological peculiarities that reflect the demands of the particular niche (Sharova 1975; Erwin et al. 1979; Forsythe 1981; Lövei & Sunderland 1996; Bauer et al. 1998; Talarico et al. 2007; Kotze et al. 2011; Kamenova et al. 2015). All carabid beetles show structural adaptations of their feeding apparatus indicative of their food preferences (Forsythe 1982, 1983; Evans & Forsythe 1985; Talarico et al. 2018). It has been suggested that the size, bulk and strength of the Carabini may help them overcome the environmental resistance (Heydemann 1957) of a variety of habitats and enable them to overcome larger but slower prey such as molluscs, worms, caterpillars and other slow-moving animals (Forsythe 1991).

Siagona europaea Dejean is exclusively myrmecophagous, feeding on both adult ants and their brood (Brandmayr & Pizzolotto 1990; Zetto Brandmayr &

*Correspondence: P. Brandmayr, Department of Biology, Ecology and Earth Science (DiBEST), University of Calabria, Arcavacata di Rende, (CS), Cosenza 87030, Italy. Tel: +390984492978. Fax: +390984492986. Email: pietro.brandmayr@unical.it

Pizzolotto 1994; Zetto Brandmayr et al. 1998; Bauer et al. 2005). It is a West Palaearctic element, widely spread from the Canary Islands and Iberian Peninsula to north-west India, including the main Mediterranean Islands – Sardinia, Sicily, Cyprus – and is known from all countries of the Balkan peninsula, all countries of Maghreb (Morocco, Algeria, Tunisia), Egypt and Libya, Caucasus, European and Asiatic Turkey, the Middle East and Central Asia (Löbl & Löbl 2017). In Southern Italy, *S. europaea* occurs in pastures and abandoned fields only in clayey soils up to an altitude of about 250 m above sea level (asl), while in Calabria it occurs up to ca. 450 m (Pizzolotto et al. 2005). In early spring, when soil moisture is high, the beetles are found under stones. From mid-April onwards, when the soil dries out and becomes deeply fissured, they retreat into deeper crevices, especially during the hot and dry hours of the day. *Siagona europaea* is an olfactory hunter and belongs to the third group of nocturnal species described by Bauer and Kredler (1993). Its activity is mainly nocturnal, as shown by recordings and by the structure of its compound eyes (Bauer et al. 2005), with a value of ommatidia/mm body length typical for nocturnal species (Talarico et al. 2011). *Poecilus* (*Metapedius*) *pantanellii* Fiori is an Italian Appennine endemite that prefers pastures and abandoned fields only in clayey soils up to an altitude of about 450 m asl. It is a beetle closely tied to the clay soils of the "calanchi" badlands, erosional forms distributed along the entire Apennine chain, and represents an example of an ecological link mediated by definite pedological preferences. The biology of this species is poorly known; both adults and larvae are generalist predators, hunting various species of invertebrates and showing nocturnal activity (Aloise et al. 2005; Brandmayr et al. 2005; Mazzei et al. 2012). *Siagona europaea* is a specialised ant hunter that seems to move easily in soil crevices, while *P.* (*M.*) *pantanellii* represents the "normal" life form of a surface runner in Carabidae (Figure 1). In this study we demonstrate that the two species share the same habitat, but we hypothesise a fully different use of space and try to relate it to their body proportions and morpho-functional features.

Material and methods

Habitats

To clarify the habitat preferences of the two species we re-elaborated our carabid community year sample databank of Calabria, by crossing vegetation characteristics with soil/substrate features. For this purpose we selected all sites where the two species were collected by pitfall traps (represented by at least one specimen) and constructed a vegetation/soil matrix of the yearly activity density values, expressed as individuals/trap in a standard period of 10 days. The year samples at disposal were 93 and ranged from a few metres in altitude up to 1600 m asl. They are mainly distributed in Central Calabria over an area of about 2500 km^2 and were collected from 1987 to 2010. The trapping season varied from 12 months at lower altitudes to 7–8 months in mountain habitats.

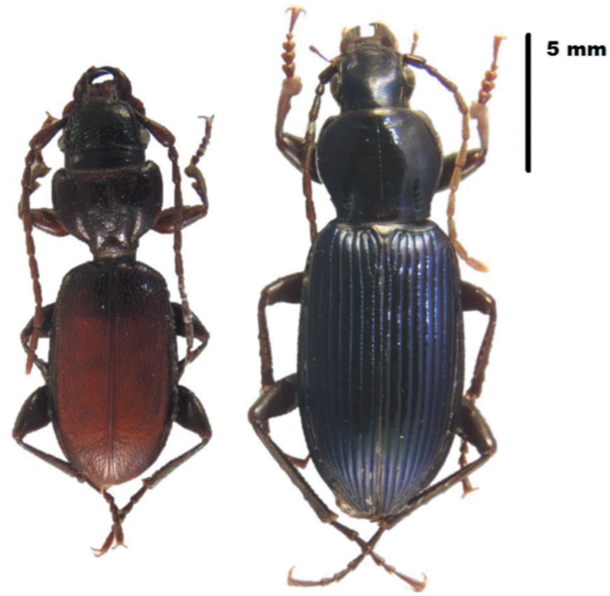

Figure 1. Habitus of specimens of: A, *Siagona europaea*; B, *Poecilus* (*Metapedius*) *pantanellii.*

Space use

For the space-use investigation we chose a clay soil pasture rich in French Honeysuckle (*Hedysarum coronarium*), where both species were present with a satisfactory population density (Calabria, Squillace, Catanzaro, 250 m asl, UTM 33 S 632065.84 m E 4294702.67 m N). Here we put in place from May to the first decade of June a first set of 13 epigean live pitfalls, with an upper diameter of 9 cm and 11 cm in depth, baited with a vial containing fruit juice and beer (Zetto Brandmayr et al. 2007). When the clay soil began to dry out (June–October) and crevices began to widen, a new set of live pitfall traps was put in place at different levels with respect to the soil surface: level 0 (epigean, seven traps); level 1, at 20–25 cm depth (hypogean, seven traps); level 2, at 35–50 cm depth (hypogean, nine traps). In June and July these traps were emptied weekly to avoid cannibalism; later, the activity density of the beetles was much lower. In winter the soil was subject to solifluction; in late spring/summer the soil was rich in crevices of 3–10 cm, and the habitat faced south with a slope of 12–15 degrees.

Animals

The sample consisted of 20 individuals (10 males and 10 females) of the two species: *S. europaea* and *P.* (*M.*) *pantanellii*. Most individuals were collected in the same pasture described above, some in neighbouring but similar pastures.

Morphometric analyses

The animals were stored in alcohol (70%). Photographs were taken with a stereoscope (Zeiss Stemi SV 11Apo) and acquired using Matrox PC-VCR software (for Windows® 2000). For each individual, we measured body length (mm), antenna length (mm), head width (mm) and head length (mm), thorax width (mm) and thorax length (mm), trochanter length (mm) and trochanter width (mm), head height (mm), thorax height (mm), and abdomen height (mm), elytra length (mm), eyes distance (mm) and antenna/eye angle (degrees). Relative measurements of antenna length, eye distance and antenna/eye angle were weighted against head width, while all measurements were weighted against body length. Measurements were taken using Sigma Scan Pro 5 Software (SPSS® Inc.).

Statistical analyses

Sexual dimorphism and morphological differences among species was tested using the Kruskal–Wallis test (Sokal & Rohlf 1995). Means are reported with the standard error of the mean (± SEM) throughout the text. Statistical analyses were performed using the Statistical Package for Social Sciences 13.01 (SPSS® Inc.).

Results

Habitat and space use

The annual activity density of *S. europaea* populations is concentrated in *Hedysarum* and *Cynara* pastures or open lands derived from cropland abandonment, but only on clay-rich soils (Table I). This species also endures a soft shadowing given by *Eucalyptus* or olive trees and a moderate sodium chloride content of the clay, and shows higher densities in the "calanchi" badlands on solifluction grounds. *Poecilus pantanellii* populations show a slightly more restricted habitat affinity; the highest density was found in a durum wheat crop on moderately salty clays derived from the mechanical levelling of clay badlands. This species absolutely avoids shadowing by trees and has never been found in olive growths or in *Eucalyptus* plantations.

Phenology and space use of the two species are extremely different: *S. europaea* remains inactive in crevices or under stones until the first half of May; thereafter it appears on the soil surface and shows an activity peak in June. In July the epigean activity is declining, but some few specimens are collected in traps until October. In June a conspicuous part of the population shifts deeper into the soil and shows a lively locomotion in the subsoil, where the capture numbers are higher than on the soil surface. In the summer months the epigean versus hypogean activity ratio is L0 – 20%, L1 – 28%, L2 – 52%; thus, the large majority of captures come from the subsoil environment (Figure 2).

Poecilus pantanellii appears in the traps in the early spring, has a peak in April/May and disappears in June, after the females cease egg laying. The larvae show a rapid development in spring/early summer, as in several spring breeders. Over the course of the year 2003 the captures were partitioned as follows: L0 – 86%, L1 – 5%, L2: 9%.

Morphometric analyses

The species investigated presented some sex differences related to size (Table II). Males of *S. europaea* have significantly longer trochanters, greater thorax height (relative to body length) and wider antenna/eye angle (relative to head width) compared to females (respectively, $X^2 = 5.851$, df = 1, $p = 0.016$; $X^2 = 8.251$, df = 1, $p = 0.004$ and $X^2 = 14.286$, df = 1, $p = 0$). Females of *S. europaea* have significantly longer bodies, elytra and heads (respectively, $X^2 = 9.394$, df = 1, $p = 0.002$; $X^2 = 6.812$, df = 1, $p = 0.009$ and $X^2 = 6.04$, df = 1, $p = 0.014$), as well as greater head width, head height, thorax width and eye distance (respectively, $X^2 = 6.807$, df = 1, $p = 0.009$; $X^2 = 6.616$, df = 1, $p = 0.01$; $X^2 = 5.5$, df = 1, $p = 0.019$ and $X^2 = 5.323$, df = 1, $p = 0.019$).

In *P.* (*M.*) *pantanellii* the females have a significantly longer body, elytra and head, and a thicker thorax and abdomen (respectively, $X^2 = 8.949$, df = 1, $p = 0.003$; $X^2 = 9.15$, df = 1, $p = 0.002$; $X^2 = 5.143$, df = 1, $p = 0.023$; $X^2 = 9.143$, df = 1, $p = 0.002$ and $X^2 = 4.806$, df = 1, $p = 0.028$). The thorax and

Table I. Vegetation versus bedrock and/or soil type in the 93-year samples examined in Calabria, and population size of *Siagona europaea* and *Poecilus pantanellii* expressed as individuals/trap in the standard period of 10 days (annual activity density). Grey cases represent combinations actually sampled; the first column indicates the number of year samples for each habitat category; numbers in parentheses indicate the number of sites in which the species was found. Where the activity is the mean of more than one sample site, the standard deviation is reported in parentheses. Extracted from the carabid community database of Calabria (Brandmayr, Mazzei and Pizzolotto, unpublished).

			Soil/substrate type											
Species	Habitat/biome	N = 93	Granite rocks	Schists	Calcareous	Sandstones and sands	Sands and clay	Pure clay badlands	Sodium chloride clays	Sulphur-rich clays	Gravels	Loose sands	Loams	Alluvium
Siagona europaea	Beech forest	10												
	Laricio pine forest	6												
	Deciduous oak forest	10												
	Chestnut forest	7												
	Holm and cork oak forest	8												
	Eucalyptus plantations	1					**0.01**							
	Shrubs and macchia	2												
	Pastures and open lands	10												
	Hedysarum/*Cynara* pastures	7(4)					**0.01**	**0.33**	**0.053** (± .05)					
	Abandoned cropland	4(2)					**0.114** (± .08)							
	Durum wheat cropland	1							**0.005**					
	Olive groves	14(2)						**0.039** (± .02)						
	Orange growths	1												
	Fiumara/river beds	12												
Poecilus pantanellii	Beech forest	10												
	Laricio pine forest	6												
	Deciduous oak forest	10												
	Chestnut forest	7												
	Holm and cork oak forest	8												
	Eucalyptus plantations	1												
	Shrubs and macchia	2												
	Pastures and open lands	10												
	Hedysarum/*Cynara* pastures	7(4)					**0.01**	**0.094**	**0.003** (± .02)					
	Abandoned cropland	4(2)					**0.021** (± .02)							
	Durum wheat cropland	1							**0.219**					
	Olive groves	14												
	Orange growths	1												
	Fiumara/river beds	12												

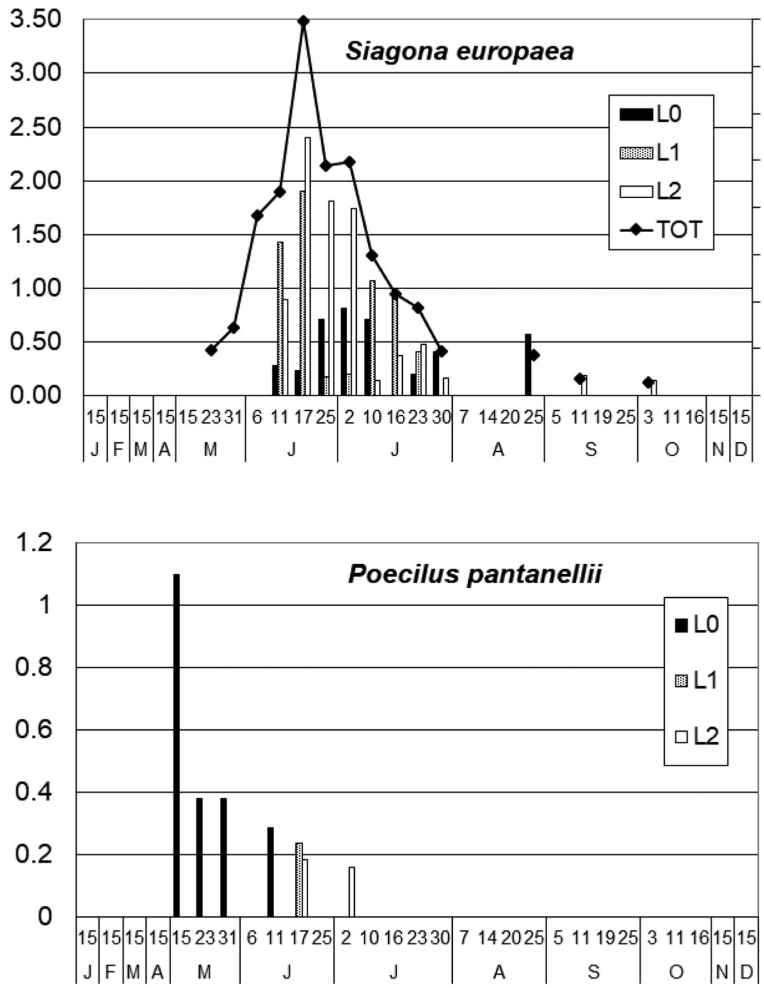

Figure 2. Phenology in relation to space use in *Siagona europaea* and *Poecilus pantanellii*. Right axis: activity density in both species (individuals/trap in the standard period of 10 days) measured at the three soil levels. L0 – soil surface; L1 – 20–25 cm depth; L2 – 35–50 cm depth. For *S. europaea* the activity density of the entire population is also plotted (left axis above). Observation year: 2003; sampling site: Squillace (CZ).

abdomen are wider and the eye distance greater than in males (respectively, $X^2 = 10.08$, df = 1, p = 0.001; $X^2 = 7.011$, df = 1, p = 0.008 and $X^2 = 7.829$, df = 1, p = 0.005). The males of *P. pantanellii* show significantly longer trochanters, a wider thorax, a greater head width and height (relative to body length), and a wider antenna/eye angle (relative to head width) compared to females (respectively, $X^2 = 3.863$, df = 1, p = 0.049; $X^2 = 7.406$, df = 1, p = 0.007; $X^2 = 8.691$, df = 1, p = 0.003 and $X^2 = 5.143$, df = 1, p = 0.023).

There are significant differences between the two species for almost all measured parameters (Table III). *Siagona europaea* shows a significantly longer and wider head, longer antennae and a greater eye distance (respectively, $X^2 = 24.775$, df = 1, p = 0; $X^2 = 24.242$, df = 1, p = 0; $X^2 = 25.861$, df = 1, p = 0; $X^2 = 29.279$, df = 1, p = 0) than *P. pantanellii*. The latter species has significantly longer and wider trochanters, a wider abdomen, longer elytra, a greater thorax height and a wider eye/antenna angle than *S. europaea* (respectively, $X^2 = 29.282$, df = 1, p = 0; $X^2 = 24.384$, df = 1, p = 0; $X^2 = 5.799$, df = 1, p = 0.016; $X^2 = 13.244$, df = 1, p = 0; $X^2 = 29.133$, df = 1, p = 0 and $X^2 = 16.415$, df = 1, p = 0).

In terms of weighted values, in *S. europaea*, antenna, head, trochanter and elytra were longer, head, abdomen and eye distance were wider and thorax and abdomen height were greater than in *P. pantanellii* (respectively, $X^2 = 9.482$, df = 1, p = 0.002; $X^2 = 13.5$, df = 1, p = 0; $X^2 = 4.86$, df = 1, p = 0.027; $X^2 = 7.073$, df = 1, p = 0.008; $X^2 = 7.45$, df = 1, p = 0.006; $X^2 = 9.918$, df = 1, p = 0.002; $X^2 = 10.364$, df = 1, p = 0.001; $X^2 = 10.591$, df = 1,

Table II. Sex differences in morphological characteristics (means and standard error of means, SEM) in the two species. Kruskal–Wallis test results are shown. Statistically significant results are in bold.

		Gender						
		Female		Male		Kruskal–Wallis test		
Species		Mean	SEM	Mean	SEM	Chi-square	df	p
Siagona europaea	Body length	12.305	0.112962	11.598	0.120386	9.394	1	**0.002**
	Antenna length	7.029	0.197553	7.3179	0.049164	0.023	1	0.88
	Head length	2.5836	0.027871	2.4872	0.030430	6.04	1	**0.014**
	Head width	2.7161	0.033838	2.5869	0.025743	6.807	1	**0.009**
	Thorax width	3.2047	0.040459	3.0593	0.034355	5.5	1	**0.019**
	Thorax length	2.4957	0.051324	2.4442	0.043793	0.63	1	0.427
	Thorax height	1.6531	0.032112	1.6482	0.017499	0.036	1	0.85
	Head height	1.3239	0.019564	1.1979	0.033786	6.616	1	**0.01**
	Abdomen height	1.7529	0.036371	1.6808	0.047163	2.403	1	0.121
	Abdomen width	3.927	0.063439	3.675	0.038571	8.264	1	**0.004**
	Trochanter length	0.8438	0.025462	0.8689	0.020205	0.143	1	0.705
	Trochanter width	0.3306	0.009774	0.3499	0.016260	1.654	1	0.198
	Elytra length	6.6015	0.082290	6.297	0.061874	6.812	1	**0.009**
	Eyes distance	2.1409	0.031511	2.0377	0.026688	5.323	1	**0.021**
	Eye/antenna angle	28.7	0.667499	40	1.173787	14.394	1	0
	Weighted antenna length	2.722291163	0.076437	2.947772	0.052080	3.023	1	0.082
	Weighted head length	0.209985753	0.001557	0.214505	0.002106	1.463	1	0.226
	Weighted head width	0.220836291	0.002887	0.223221	0.002859	0.823	1	0.364
	Weighted thorax width	0.260590478	0.003691	0.263990	0.003702	0.366	1	0.545
	Weighted thorax length	0.202871524	0.003953	0.210688	0.00257555	1.12	1	0.29
	Weighted thorax height	0.134251024	0.001583	0.14213523	0.0009261	8.251	1	**0.004**
	Weighted head height	0.107700071	0.002072	0.10325297	0.00256175	0.966	1	0.326
	Weighted abdomen height	0.319241796	0.004980	0.14522584	0.00489443	0.006	1	0.94
	Weighted abdomen width	0.319241796	0.004980	0.31709132	0.00396333	0.366	1	0.545
	Weighted trochanter length	0.068657288	0.002256	0.07489505	0.00140302	5.851	1	**0.016**
	Weighted elytra length	0.536789135	0.007462	0.54337392	0.00705938	0.091	1	0.762
	Weighted eye distance	0.828820318	0.009821	0.81929426	0.00428608	1.651	1	0.199
	Weighted eye/antenna angle	11.10468204	0.205716	16.1487892	0.64254156	14.286	1	**0**
Poecilus (*M.*) *pantanellii*	Body length	12.574	0.247616	11.194	0.22152602	8.949	1	**0.003**
	Antenna length	5.6628	0.239358	5.3186	0.20366051	1.12	1	0.29
	Head length	2.2476	0.060684	2.0574	0.03249793	5.143	1	**0.023**
	Head width	2.2002	0.041061	2.1396	0.08130603	2.522	1	0.112
	Thorax width	3.3402	0.054035	3.1104	0.03054985	10.08	1	**0.001**
	Thorax length	2.7482	0.079216	2.5544	0.10044923	1.853	1	0.173
	Thorax height	2.4696	0.060038	2.1127	0.07365204	9.143	1	**0.002**
	Head height	1.2719	0.014355	1.2861	0.04197815	0.174	1	0.677
	Abdomen height	2.5818	0.091901	2.1708	0.13370696	4.806	1	**0.028**
	Abdomen width	4.348	0.080021	3.8635	0.10680993	7.011	1	**0.008**
	Trochanter length	1.3095	0.053756	1.3615	0.01946749	0.013	1	0.91
	Trochanter width	0.5132	0.0058	0.4726	0.02192877	2.526	1	0.112
	Elytra length	7.5625	0.123101	6.727	0.15288194	9.15	1	**0.002**
	Eye distance	1.5172	0.023841	1.3933	0.03366371	7.829	1	**0.005**
	Eye/antenna angle	43	1.437590	46.3	1.67365202	1.483	1	0.223
	Weighted antenna length	2.512801984	0.051378	2.57923761	0.06364198	0.366	1	0.821
	Weighted head length	0.178621698	0.002476	0.18402285	0.00221127	0.691	1	0.406
	Weighted head width	0.175231831	0.002934	0.19091626	0.00496493	7.406	1	**0.007**
	Weighted thorax width	0.265977092	0.003230	0.27846549	0.00394353	3.863	1	**0.049**
	Weighted thorax length	0.218850213	0.006175	0.22769204	0.00540102	1.463	1	0.226
	Weighted thorax height	0.196679027	0.004610	0.18833611	0.00340608	2.063	1	0.151
	Weighted head height	0.101503315	0.002305	0.11499281	0.00350623	8.691	1	**0.003**
	Weighted abdomen height	0.204882644	0.004207	0.19299527	0.00955847	1.12	1	0.29
	Weighted abdomen width	0.345962752	0.002922	0.34483192	0.00436873	0.023	1	0.88
	Weighted trochanter length	0.104522566	0.004859	0.12182106	0.00163374	9.606	1	**0.002**
	Weighted elytra length	0.601993693	0.005511	0.60238484	0.01538890	0.051	1	0.821
	Weighted eye distance	0.677816465	0.014036	0.67686495	0.00977169	0.091	1	0.762
	Weighted eye/antenna angle	19.31545316	0.971872	22.5489297	0.88341662	5.143	1	**0.023**

Table III. Inter-specific differences in morphological characteristics (means and standard error of the mean, SEM) in the two species. Kruskal–Wallis test results are shown. Statistically significant results are in bold.

	Siagona europaea		*Poecilus (M.) pantanellii*				
	Mean	SEM	Mean	SEM	Chi-square	df	p
Body length	11.9515	0.1141565	11.884	0.22627928	0.144	1	0.705
Antenna length	7.17345	0.1044699	5.4907	0.15796125	25.861	1	**0**
Head length	2.5354	0.0229255	2.1525	0.03997910	24.775	1	**0**
Head width	2.6515	0.0254519	2.1699	0.04487015	24.242	1	**0**
Thorax width	3.132	0.0307476	3.2253	0.04009266	2.869	1	0.096
Thorax length	2.46995	0.0333617	2.6513	0.06610733	3.19	1	0.074
Thorax height	1.65065	0.0178068	2.29115	0.06176194	29.133	1	**0**
Head height	1.2609	0.0238730	1.279	0.02165215	0.002	1	0.968
Abdomen height	1.71685	0.0301422	2.3763	0.09196263	18.5	1	**0**
Abdomen width	3.801	0.0462723	4.10575	0.08548258	5.799	1	**0.016**
Trochanter length	0.85635	0.0160791	1.3355	0.02845610	29.282	1	**0**
Trochanter width	0.34025	0.0094948	0.4929	0.01198110	24.384	1	**0**
Elytra length	6.44925	0.0610783	7.14475	0.13531370	13.244	1	**0**
Eye distance	2.0893	0.0233239	1.45525	0.02459694	29.279	1	**0**
Eye/antenna angle	34.35	1.4532631	44.65	1.13850086	16.415	1	**0**
Weighted antenna length	2.83503	0.0519147	2.54601980	0.04052865	9.482	1	**0.002**
Weighted head length	0.21224	0.0013762	0.18132227	0.00173040	13.5	1	**0**
Weighted head width	0.22202	0.0019963	0.18307404	0.00333395	9.918	1	**0.002**
Weighted thorax width	0.26229	0.0025742	0.27222129	0.00286468	3.311	1	0.069
Weighted thorax length	0.20677	0.0024649	0.22327113	0.00411941	4.86	1	**0.027**
Weighted thorax height	0.13819	0.0012706	0.19250757	0.00294931	7.642	1	**0.006**
Weighted head height	0.10547	0.0016828	0.10824806	0.00256227	2.821	1	0.093
Weighted abdomen height	0.14383	0.0027095	0.19893896	0.00526228	10.82	1	**0.001**
Weighted abdomen width	0.31816	0.0031073	0.34539733	0.00256114	10.364	1	**0.001**
Weighted trochanter length	0.07177	0.0014777	0.11317181	0.00318788	7.073	1	**0.008**
Weighted elytra length	0.54008	0.0050559	0.60218927	0.00795527	7.45	1	**0.006**
Weighted eye distance	0.82405	0.0053285	0.67734070	0.00832401	10.591	1	**0.001**
Weighted eye/antenna angle	13.6267	0.6652684	20.9321914	0.73899540	5.016	1	**0.025**

$p = 0.001$; $X^2 = 7.642$, $df = 1$, $p = 0.006$ and $X^2 = 10.82$, $df = 1$, $p = 0.001$). In contrast, *P. pantanellii* has a longer thorax and a wider antenna/eye angle than *S. europaea* (respectively, $X^2 = 4.86$, $df = 1$, $p = 0.027$ and $X^2 = 5.016$, $df = 1$, $p = 0.025$).

Discussion

Siagona europaea and *P. pantanellii* show a strong overlap in habitat. The two species live together in most kinds of open Mediterranean habitats, if the soil is prevalently clayey; other soil types are carefully avoided. The two beetles were present in only 11 of 93 sites and *P. pantanellii* has been found to be syntopic with *S. europaea* in six of 10 sites; the second species appears less stenoecious because it is able to colonise moderately shadowed habitats such as olive growths and *Eucalyptus* reforestations. The space use and phenology of *P. pantanellii* populations appear quite different from those of *S. europaea*. The former species is extremely active only in early spring, especially in April and May, when the clay surface is still wet and more compact and the females are rapidly laying their eggs in the first small soil cracks; in summer the population immediately declines and subterranean activity is minimal. Conversely, the locomotory activity of *S. europaea* peaks later, in June and July, when the soil cracks widen, and about 80% of the adults shift their activity into the subsoil. Here, the adults and the blind larvae (Zetto Brandmayr et al. 2007) catch especially worker ants exploring the crevice system around their nests; meanwhile, the females probably try to lay their eggs in the neighbourhood of the nest entrances (Bauer et al. 2005).

In the results, we highlight sex and inter-specific differences in the two species investigated. *Siagona europaea* is an olfactory hunter and belongs to the third group of nocturnal species described by Bauer and Kredler (1993). In particular, differences in antenna length reflect different sensory habits, as the antennae are usually longer in tactile than in visual hunters (Bauer & Kredler 1993). The antennae are longer in *S. europaea* than in *P. pantanellii*, suggesting that the first species bases its predation behaviour on more tactile cues (Figure 3).

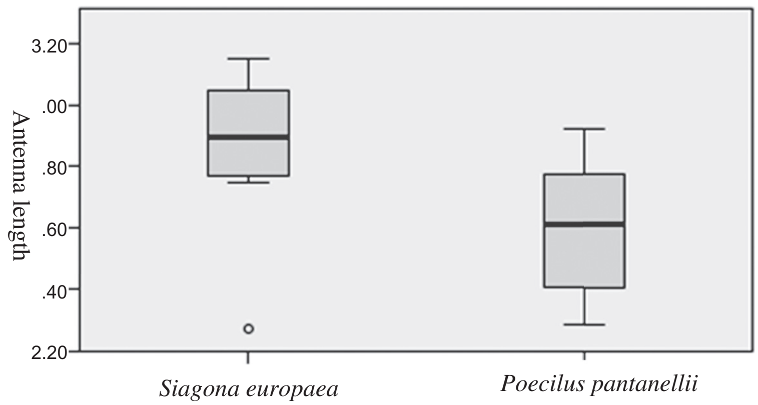

Figure 3. Measured trait of antenna length (mm) in the two species.

Concerning locomotion, as suggested by Forsythe (1991), "wedge pushers" are equipped with long trochanters, enabling them to push their body under the litter in search of prey. Our results confirm that *P. pantanellii* preys under the litter layer, thanks to its longer trochanters, while *S. europaea* moves between the natural crevices of the soil in search of prey. The measurements show that *P. pantanellii* has a greater eye/antenna angle than *S. europaea* (Figure 4). Eye/antenna angle reflects both the eye size and the position of the antennae with respect to the eyes. Species with a wider eye/antenna angle are typically visual hunters, while olfactory/tactile hunters have a smaller angle (Bauer & Kredler 1993; Bauer et al. 1998). However, further investigation of eye components is needed to confirm this thesis.

In relation to thorax and abdomen height, we found that *S. europaea* has a much flatter body than *P. pantanellii* (Figure 5A–B). A thin body and thoracic constriction are obvious adaptations to life in narrow soil crevices. *Siagona europaea* occurs in open land on clay soils. In early spring, when soil moisture is high, the beetles aggregate motionless under stones, but from mid-April onwards, when the soil dries out and becomes deeply fissured, they retreat into deeper crevices, especially during the hot, dry hours of the day. Their flat body clearly indicates an adaptation to life in clay soil crevices, surely at least 50 cm below the soil surface, as we can suppose by the position of our traps, but perhaps also deeper.

Our measurements confirm that the body size differences between the two species studied suit their different habits, their phenology and the space use they display. Indeed, *S. europaea* is a specialised ant hunter that seems to move mainly in soil crevices thanks to a very flat body, while *P.* (*M.*) *pantanellii* represents the "normal" life form in Carabidae,

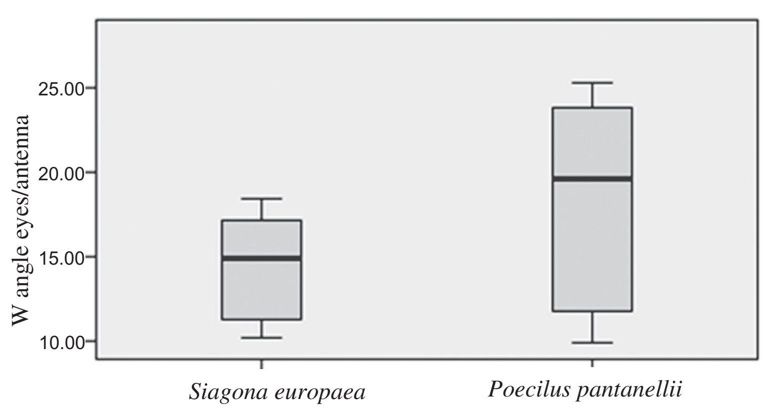

Figure 4. Measured trait of weighted antenna/eye angle (in degrees) in the two species.

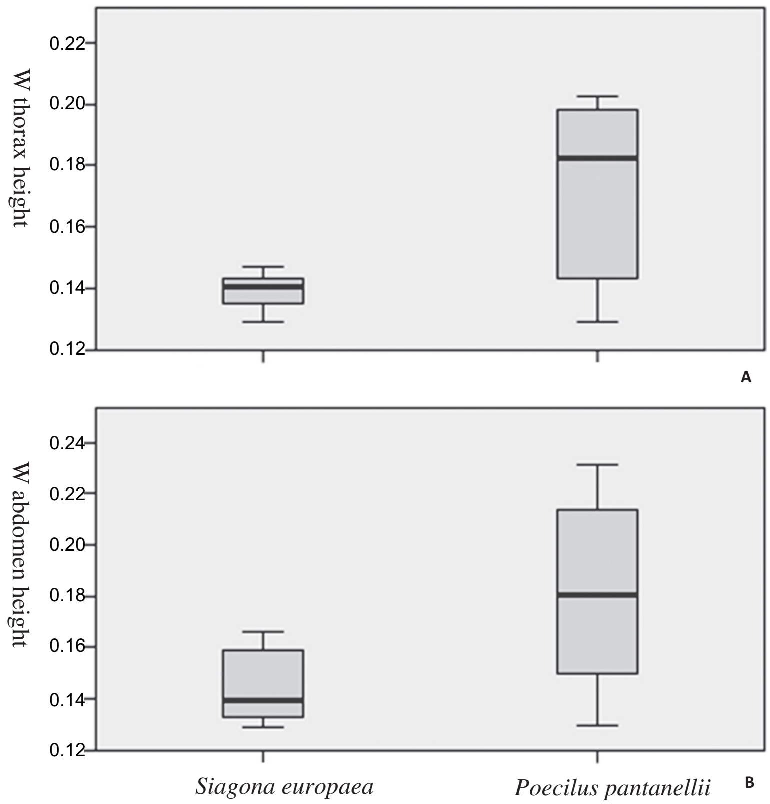

Figure 5. Measured traits: A, weighted thorax height; B, weighted abdomen height (mm) in the two species.

preying in epigean fashion on the soil surface, and shows the characteristics of species belonging to the first and second groups of Bauer and Kredler (1993). Further differences are found at egg-laying time, which happens very early in spring in *P. pantanellii*, and somewhat later in *S. europaea* (end of May, June), and in the body colour, which is bright blue in the former beetle and brownish-black in the latter. Both species seem well adapted to the unstable habitat conditions of the clay soils, which are marked by strong solifluction during the winter rain season. Features in common are the full-sized wings, related to high dispersal power and thus the ability to react to sudden soil watering (Den Boer et al. 1980). *Siagona europaea* in fact differs from other Mediterranean species of the same genus (*S. jenissoni* Dejean, *S. dejeani* Rambur) that are short winged and have a lower number of ommatidia (Talarico et al. 2011); thus, it is probable that other representatives of this Afro-Indian and Mediterranean genus are more closely adapted to the subsoil environment of pastures and clayey badlands. A further proof of the trend towards eye reduction in *Siagona* was found in a recently described species, *S. taggadertensis* Junger & Faille, from a cave in Morocco, which is marked by an extremely robust head with noticeably small and flat eyes (Junger & Faille 2011). *Siagona europaea* and *P. pantanelli* belong to two very different carabid lineages, but they live syntopically, especially in the Southern Italian clay badlands. Here, the first species is exploiting the deep fissure system, the second the favourable watering conditions of the short, early spring. *Siagona europaea* represents a "northern" borderline element of an ancient subtropical genus that was able to become more widespread in more Mediterranean countries. *Poecilus pantanellii* is a recent Italian endemite that conserved its flying ability in relation to the watering demands of the habitat, which require the maintenance of useful wings.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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