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Morphometry and eye morphology in three species of *Carabus* (Coleoptera: Carabidae) in relation to habitat demands

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Abstract

Morphological features of three common European olfactory hunting carabid beetles, *Carabus coriaceus mediterraneus* Born, 1906, *Carabus lefebvrei* Dejean, 1826 and *Carabus preslii neumeyeri* Schaum, 1856, were compared. According to eye measurements, the three species are nocturnal and/or twilight hunters. They differ, however, in relative length of the antennae, relative surface area of the compound eyes, density of ommatidia and relative head width. These differences can be correlated with the species-specific habitat demands (light intensity, open land or shaded places). In particular, the greater lateral eye protrusion in *C. lefebvrei* corresponds to its tree-climbing habits, while the larger relative eye surface area and ommatidia density in *C. coriaceus* correspond to its choice of open habitats.

Key words: compound eyes – morphometric measurements – *Carabus*

Introduction

Morphological characters of the compound eye reflect features of the life-style of insect species (Wehner 1981), and thus can be used to infer such features (Bauer and Kredler 1993). For inhabitants of the deep litter layer and/or caves, eyes may be superfluous, or it may be sufficient to them to perceive the direction of a light source, as these species usually need to avoid bright light (for a review see Bartkowiak et al. 1991). Surface-dwelling species, however, should be able to orient themselves with respect to the surrounding vegetation and landscape features. If they are active during the night or at twilight, they should at least be capable of perceiving variations in light intensity and large silhouettes in their surroundings, to remain in their habitat or to find another into which they can migrate (Lauterbach 1964; Bathon 1973). Krumbiegel (1932) showed geographic (N/S and E/W) variation correlated to day/night activity in relation with the size of the eyes. He found measurable differences in the photophoby/diurnal activity of western and eastern populations of *Carabus nemoralis* Müller, 1764. The eyes of populations of East Europe were smaller and conical, the activity full nocturnal. If a species is active in the daylight, it is threatened by visual hunting predators, such as birds and other insects (e.g. Pearson 1985), and must be able to perceive small moving silhouettes. Visual hunting ground beetles, which regularly move in the light to seek prey, must not only be able to perceive predators (i.e. objects usually larger than themselves) but also to prey upon animals smaller than themselves. In addition, they should be able to guess the distance and absolute size of the prey before an attack (Bauer 1981, 1985; Schwind 1989).

Diurnal visual hunters have large, laterally protruding eyes with distinct binocular overlap of the visual fields. In nocturnal insects that detect prey chemically and by mechanical cues, the eyes are much smaller with fewer ommatidia (Bauer et al. 1998).

All species of carabid beetles show structural adaptations of their feeding apparatus indicative of their feeding habits (Forsythe 1982, 1983; Evans and Forsythe 1985). There is also a direct correlation between body form and habitat (e.g. feeding, locomotion, burrowing and flight). For instance, the Carabini are generally heavier, bulkier and stronger than other running ground beetles, but also relatively slow runners. This is reflected mainly in the size of the hind body, notably hind body depth and prothorax depth. 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).

Species that propel themselves through the litter when searching for prey generally have much larger trochanters than surface runners (Forsythe 1991).

The members of the genus *Carabus*, which includes > 800 species, show well-developed differentiation at population level. In some species, more than several dozen subspecies have been described. The differentiation mainly involves elytral sculpture and colour. For these characters, as well as for many morphometric parameters, random drift seems to be the driving force of differentiation below the species level (Assmann et al. 2000).

The beetles of the genus *Carabus* are mostly nocturnal olfactory/tactile predators that run on the surface of soil or litter (Grüm 1976). They may compete for food with similarly sized carabid beetles of the genera *Calosoma* and *Cychrus* (Grüm 1994).

According to Casale et al. (1982), many *Carabus* species are specialized for snail hunting. Such species have a slender forebody ('cychrization', e.g. *Carabus cychroides* Baudi, 1860) and enter the shell through the aperture to attack the gastropod.

Another important strategy is shell-breaking, as described for *Carabus coriaceus* Linnaeus, 1758 (Sturani 1962).

In Italy, the habitat of *C. coriaceus* includes various lowland and hill biotopes, including urban habitats such as parks and gardens. It is mostly diurnal in autumn (September to October), especially during rainy days (Turin et al. 2003). *Carabus lefebvrei* Dejean, 1826 inhabits forests and forest edges, from sea level (*Quercus* spp.) and foothills (*Castanea*) to montane forests (*Fagus sylvatica* at 800–1800 m asl and coniferous stands at 900–2000 m asl). This is a nocturnal species and hides under stones or climbs trees during the day. Activity begins in mid-March (Sicily) but increases in April and continues until summer (Korell 1975). In Italy, *Carabus preslii* Dejean & Boisduval, 1830 prefers montane forests from 500 to 1800 m asl. It occurs in deciduous (*Fagetum*) and coniferous forests, but is less common in broad-leafed forests (Casale et al. 1982).

In this study, we investigated three species of the genus *Carabus*: *C. coriaceus mediterraneus* Born, 1906 (Fig. 1a), *C. lefebvrei* Dejean, 1826 (Fig. 1b) and *C. preslii neumeyeri* Schaum, 1856 (Fig. 1c). These species differ greatly in colour, habitus and habitat choice. We assume that *C. coriaceus* is an open habitat species adapted to very high light intensity, whereas the other species prefer shaded places. We tested the hypothesis that the supposed differences in habitat demands are reflected by differences in morphology, especially the shape and size of the compound eyes.

Materials and Methods

The sample consisted of 14 individuals (seven males and seven females) for each of the three *Carabus* species: *C. coriaceus*, *C. lefebvrei* and *C. preslii*. Specimens were collected in southern Italy (Calabria): *C. coriaceus* was caught (bait-traps) in open fields and pastures (Squillace, Catanzaro) in spring 2004 (250 m asl), while *C. lefebvrei* and *C. preslii* were trapped (pit-fall traps) in upland forests (Sila Mountains) between March and September 2003 (1200 m asl).

All specimens were stored in alcohol (70%). Photographs were taken with a stereoscope (Zeiss Stemi SV 11Apo) and acquired by Matrox PC-VCR software (Windows 2000). For each individual, we measured body length (mm), antenna length (mm), head width (mm), trochanter length (mm), number of ommatidia, eye protrusion (mm) (head width-eye distance, Fig. 2), eye surface area (mm^2), ommatidia density (number of ommatidia/mm^2 of eye surface area).

Relative measures of antenna length, number of ommatidia, eye surface area and eye protrusion were weighted against head width, while trochanter length was weighted against body length.

To determine the number of ommatidia and cornea size, we softened the specimens in hot potash lye for a few minutes. The cornea was removed and fixed through the following stations: distilled water, acetone, ethanol (70%), absolute ethanol and xylol. It was then spread on a microscope slide and photographed. Measurements were taken using Sigma Scan Pro 5 Software (SPSS®, Chicago, Inc.).

Statistical analyses

Sexual dimorphism in the morphological traits was assessed in each species using the Mann–Whitney *U*-test (Siegel and Castellan 1988),

Fig. 2. Measured traits: head width (a), eye distance (b) and eye protusion (a, b)

while ANOVA was used to test for morphological differences among species (Sokal and Rohlf 1995). Multiple comparisons (between species) were performed using the Tamhane Test for homogeneous variances not assumed.

The probability level was computed by a complete randomization method (permutation or exact test; P_{exact}) or by a Monte Carlo simulation based on 10 000 sampled tables ($P_{MonteCarlo}$) when computation was not possible (Mehta and Patel 1996; Good 2000).

Means are reported with standard error of the mean (±SEM) throughout the text. Statistical analyses were performed with the Statistical Package for Social Sciences 10.01 (SPSS® Inc.).

Results

The three species presented clear sex differences (Table 1). In *C. coriaceus*, the males had significantly longer antennae (relative length) than the females ($U = 4.0$, $W = 32.0$, $P_{exact} = 0.007$). In *C. preslii*, the males also had significantly longer antennae but a smaller head (respectively $U = 0.0$, $W = 28.0$, $P_{exact} = 0.001$, and $U = 1.0$, $W = 29.0$, $P_{exact} = 0.001$). Most interesting, *C. lefebvrei* presented sexual dimorphism in eye traits: the females had a significantly higher number of ommatidia in significantly larger and more protruding eyes than the males (respectively $U = 4.0$, $W = 32.0$,

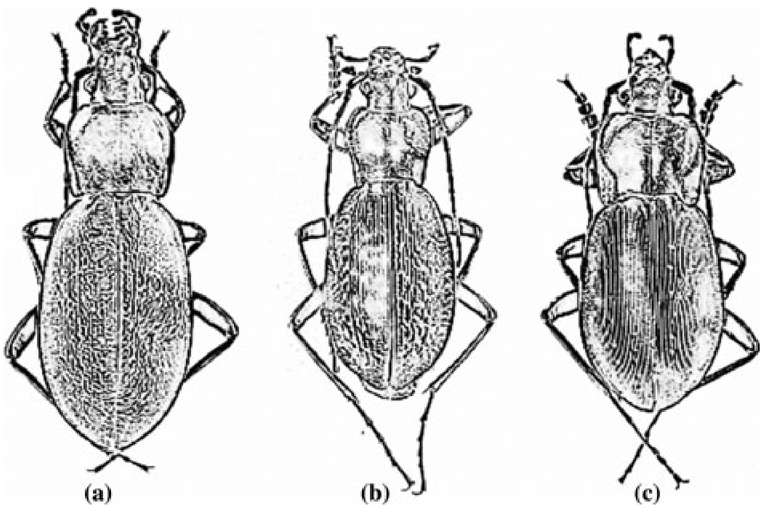

Fig. 1. Specimens of *Carabus coriaceus mediterraneus* (a), *Carabus lefebvrei* (b), *Carabus preslii neumeyeri* (c)

Table 1. Sex differences in body and eye characters (mean and standard error of the mean) in three species of *Carabus*

	Females		Males				
Measures	Mean	SEM	Mean	SEM	U	W	P_{exact}
C. coriaceus							
Body length (mm)	33.743	0.462	32.786	0.352	12.0	40.0	0.128
Antenna length (mm)	13.580	0.274	14.163	0.155	12.0	40.0	0.128
Number of ommatidia	3286.500	97.910	3361.143	88.892	18.0	46.0	0.456
Eye surface	0.765	0.034	0.666	0.039	13.0	41.0	0.165
Head width (mm)	5.167	0.080	5.036	0.061	15.0	43.0	0.259
Trochanter length (mm)	2.521	0.046	2.439	0.033	13.0	41.0	0.165
Weighted trochanter length	0.075	0.001	0.074	0.001	24.0	52.0	1.000
Weighted antenna length	2.630	0.051	2.814	0.029	4.0	32.0	**0.007**
Weighted ommatidia number	636.512	18.981	668.759	22.942	16.0	44.0	0.318
Ommatidia density (N/sqmm)	4376.594	250.588	5148.797	299.186	12.0	40.0	0.128
Weighted eye surface	0.148	0.005	0.132	0.007	14.0	42.0	0.209
Eyes protrusion/2	0.753	0.041	0.793	0.031	16.5	44.5	0.318
Weighted eye protrusion	0.146	0.008	0.157	0.006	16.0	44.0	0.318
C. lefebvrei							
Body length (mm)	28.143	0.382	25.586	0.236	0.0	28.0	**0.001**
Antenna length (mm)	13.559	0.404	13.463	0.131	22.0	50.0	0.805
Number of ommatidia	3003.143	83.042	2654.786	100.526	4.0	32.0	**0.007**
Eye surface	0.499	0.043	0.372	0.015	8.0	36.0	**0.038**
Head width (mm)	4.361	0.083	4.121	0.046	7.0	35.0	0.026
Trochanter length (mm)	2.030	0.059	1.904	0.035	10.5	38.5	0.073
Weighted trochanter length	0.072	0.002	0.074	0.001	18.0	46.0	0.456
Weighted antenna length	3.108	0.064	3.268	0.035	12.0	40.0	0.128
Weighted ommatidia number	688.559	14.242	643.508	20.508	11.0	39.0	0.097
Ommatidia density (N/sqmm)	6365.588	517.102	7348.191	421.348	13.0	41.0	0.165
Weighted eye surface	0.114	0.008	0.090	0.003	8.0	36.0	0.038
Eyes protrusion/2	0.937	0.025	0.993	0.016	11.0	39.0	0.097
Weighted eye protrusion	0.215	0.005	0.241	0.003	0.0	28.0	**0.001**
C. preslii							
Body length (mm)	25.000	0.254	24.229	0.326	12.0	40.0	0.128
Antenna length (mm)	12.073	0.290	12.897	0.198	6.0	34.0	**0.017**
Number of ommatidia	2078.214	94.479	2035.071	65.446	19.0	47.0	0.535
Eye surface	0.314	0.008	0.314	0.020	18.0	46.0	0.456
Head width (mm)	4.151	0.063	3.827	0.043	1.0	29.0	**0.001**
Trochater length (mm)	2.050	0.043	1.973	0.039	14.5	42.5	0.209
Weighted trochanter length	0.082	0.001	0.081	0.001	23.0	51.0	0.902
Weighted antenna length	2.915	0.097	3.370	0.043	0.0	28.0	**0.001**
Weighted ommatidia number	502.963	28.724	531.913	16.553	18.0	46.0	0.456
Ommatidia density (N/sqmm)	6610.511	265.837	6635.124	434.627	22.0	50.0	0.805
Weighted eye surface	0.076	0.003	0.082	0.005	13.0	41.0	0.165
Eyes protrusion/2	0.665	0.045	0.529	0.030	8.5	36.5	**0.038**
Weighted eye protrusion	0.160	0.009	0.138	0.008	12.0	40.0	0.128

Results of Mann–Whitney test, and significance levels estimated with a permutation procedure (P_{exact}). Bold, characters with significant sexual dimorphism.

$P_{exact} = 0.007$, $U = 8.0$, $W = 36.0$, $P_{exact} = 0.038$, and $U = 0.0$, $W = 28.0$, $P_{exact} = 0.001$). In *C. preslii*, the females also had significantly more protruding eyes ($U = 8.5$, $W = 36.5$, $P_{exact} = 0.038$), but the weighted eye protrusion did not differ between the sexes ($U = 12.0$, $W = 40$, $P_{exact} = 0.128$).

ANOVA revealed an overall significant difference among the three species for all the measured parameters (Table 2; ANOVA, $p < 0.001$). The multiple comparisons showed clear differences between the three species for most of the traits (Figs 3 and 4, Tamhane tests, $p < 0.001$), but not for two absolute measures (trochanter length and ommatidia density) and four relative ones (weighted trochanter length, weighted antenna length, weighted ommatidia number and weighted eye protrusion). *Carabus coriaceus* significantly differed from the other two species for weighted antenna length ($P < 0.001$); however, it was not significantly different from *C. lefebvrei* for weighted trochanter length (Tamhane test, mean difference = 0.001, p = 0.302) and weighted ommatidia number (Tamhane test, mean difference = −13.39, p = 0.884), or from *C. preslii* for weighted eye protrusion (Tamhane test, mean difference = 0.003, p = 0.985). *Carabus lefebvrei* and *C. preslii* significantly differed for all parameters except two-dimensional ones, trochanter length and weighted antenna length (respectively, Tamhane test, mean difference = −0.040, p = 0.739, and Tamhane test, mean difference = −0.045, p = 0.948), and one eye trait (ommatidia density, Tamhane test, mean difference = 234.07, p = 0.930).

Discussion

The three species present differences in both body and eye traits. All three species are olfactory hunters, but their different life-styles have influenced body and eye characteristics: *C. coriaceus* and *C. lefebvrei* can be included in the second group of Bauer and Kredler (1993), which includes species with no preferred activity period (i.e. active by day

Table 2. Inter-specific differences in body and eye characters (mean and standard error of the mean) in three species of *Carabus*. ANOVA results

	Species								
	Carabus coriaceus		*Carabus lefebvrei*		*Carabus preslii*				
Measures	Mean	SEM	Mean	SEM	Mean	SEM	*F*	df	p
Body length (mm)	33.264	0.309	26.864	0.415	24.614	0.226	189.53	2	0.000
Antenna length (mm)	13.871	0.171	13.511	0.204	12.485	0.204	13.79	2	0.000
Number of ommatidia	3323.821	64.365	2828.964	79.102	2056.643	55.535	90.74	2	0.000
Eye surface	0.716	0.028	0.435	0.028	0.314	0.010	74.55	2	0.000
Head width (mm)	5.101	0.052	4.241	0.056	3.989	0.058	111.00	2	0.000
Trochanter length (mm)	2.480	0.029	1.967	0.037	2.011	0.030	77.35	2	0.000
Weighted trochanter length	0.075	0.001	0.073	0.001	0.082	0.001	26.66	2	0.000
Weighted antenna length	2.722	0.038	3.188	0.041	3.143	0.081	20.37	2	0.000
Weighted ommatidia number	652.635	14.987	666.034	13.524	517.438	16.424	29.93	2	0.000
Ommatidia density (N/sqmm)	4762.696	215.905	6856.890	348.200	6622.818	244.770	17.34	2	0.000
Weighted eye surface	0.140	0.005	0.102	0.005	0.079	0.003	46.56	2	0.000
Eyes protrusion/2	0.773	0.025	0.965	0.016	0.597	0.032	52.51	2	0.000
Weighted eye protrusion	0.152	0.005	0.228	0.004	0.149	0.007	68.39	2	0.000

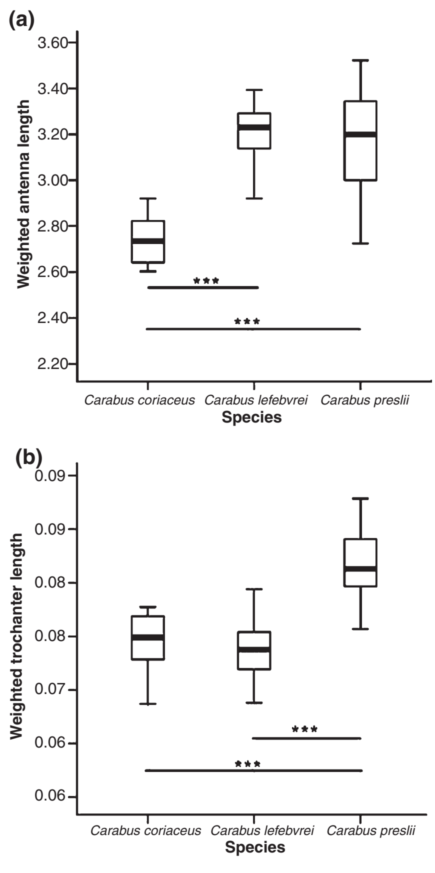

Fig. 3. Measured traits: (a) weighted antenna length (mm), (b) weighted trochanter length (mm)

and night, but preferably at twilight), while *C. preslii* belongs to the third group of nocturnal species (Bauer and Kredler 1993).

Differences in antenna length may reflect different sensory abilities/habits, as the antennae are usually shorter in visual hunters than in tactile hunters (Bauer and Kredler 1993). The relative length of the antenna (Fig. 3a) is bigger in *C. preslii* and *C. lefebvrei* than in *C. coriaceus*, suggesting that the first two species are prevalently tactile hunters.

We also found that *C. coriaceus* and *C. lefebvrei* have shorter trochanters than *C. preslii* (Fig. 3b). According to Forsythe (1991), surface runners are equipped with short trochanters, in contrast to 'wedge pushers' which seem to have relatively long and broad trochanters, enabling them to push their body under the litter layer in search of prey (Bauer and Kredler 1993). Hence our results suggest marked surface habits in *C. coriaceus* and *C. lefebvrei* (in contrast to *C. preslii*), confirming what is known about the ecology of the species (Turin et al. 2003).

We then observed that *C. coriaceus* has larger eyes than the other two species, suggesting partial visual hunter habits, since visual hunters generally have larger eyes than tactile hunters (Bauer and Kredler 1993).

There are more clearly defined differences in the number of ommatidia (Fig. 4b). Indeed, visual hunters generally have about 50% more ommatidia than tactile hunters (Bauer et al. 1998). The number of ommatidia is much larger in *C. coriaceus* than in *C. lefebvrei* and *C. preslii*, all three species differing significantly for this parameter. This confirms that *C. coriaceus* is more adapted to open habitats than the other two species.

The number of ommatidia per unit surface area of the eye (ommatidia density) varies even within the same genus, and it is probably an adaptation to the light conditions in the species-specific habitat. The number of ommatidia cannot be derived automatically from the eye surface area. The mean diameter of the facet lenses may vary between species, even if identical parts of the eye are compared. One explanation for this is that to achieve optimal contrast sensitivity the lens size is adapted to the mean light intensity under which the eyes have to function (Bauer and Kredler 1993).

Carabus coriaceus has a larger relative surface area of the eyes and a higher number of ommatidia than *C. lefebvrei* and *C. preslii*, while its ommatidia density (number/mm^2 of surface area) is lower than in the other two species. The latter finding contrasts with the trend of the other parameters (surface area and number of ommatidia).

Carabus lefebvrei shows greater eye protrusion than the other two species. Laterally, protruding compound eyes favour peripheral vision and may be associated with an array of ommatidia improving resolution in the frontal visual field (e.g. Burkhardt and de la Motte 1983). However, they may also hinder the movements of the beetle between plants and soil

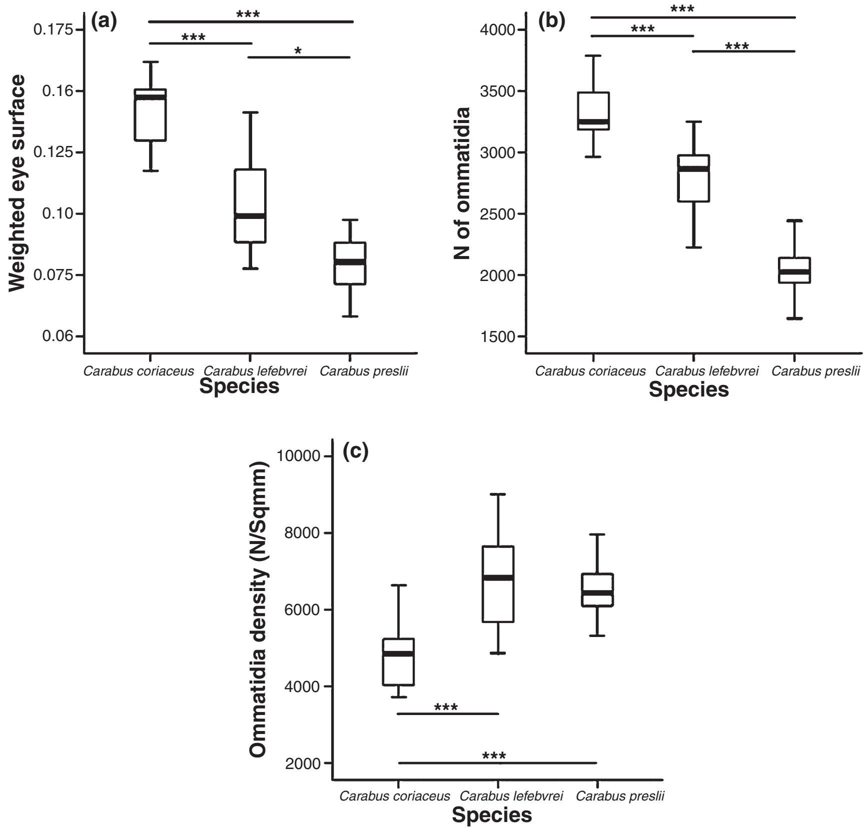

Fig. 4. Measured traits: (a) weighted eye surface area (mm^2), (b) number of ommatidia, (c) weighted ommatidia density (N/sqmm)

structures. Perhaps this finding can be explained by the fact that *C. lefebvrei* is the only one of the three species that climbs trees and probably also hunts on them.

In visual hunters, the eyes not only protrude laterally but also frontally above the bases of the antennae. In nocturnal species, the antennae are inserted more in front of the eyes, the front edges of which are often curved around the antennal bases. In this position, the antennae hinder frontal vision, indicating that, for this group, mechanical and chemical cues are much more important in detecting nearby objects (Bauer and Kredler 1993). The eye-antenna angle in the three species does not differ greatly (*C. coriaceus* mean 38.50°, *C. lefebvrei* mean 27.28°, *C. preslii* mean 36.34°) and is never > 50°, a value found only in visual hunters (Bauer and Kredler 1993).

The three species also differ in the extent of sexual dimorphism. The males of *C. coriaceus* and *C. preslii* have significantly greater relative antenna length than the females. This is found in most Carabidae and is likely related to the fact that males, rather than females, actively search for sexual partners (Bauer et al. 1998). Sexual dimorphism is even greater in *C. lefebvrei*, with the females having a significantly higher number of ommatidia and larger and more protruding eyes than males. This may reflect niche differentiation within the species, although no other data are available in this regard.

Our results confirm that morphological measurements, especially of the compound eyes, can be considered sensitive indicators of different habitat demands among closely related species.

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Riassunto

Morfometria e morfologia degli occhi in tre speciedi Carabus (Coleoptera, Carabidae) in relazione alle caratteristiche dell' habitat

Sono state investigate le caratteristiche morfometriche e dei componenti degli occhi di tre specie di coleotteri carabidi predatori olfattivi, *Carabus coriaceus mediterraneus* Born (1906), *C. lefebvrei* Dejean (1826) e *C. preslii neumeyeri* Schaum (1856). Le differenze dei parametri considerati, nelle tre specie in esame, sono riconducibili con le diverse caratteristiche dei diversi habitat sfruttati. In particolare, sono state riscontrate differenze nella protrusione laterale degli occhi, che è maggiore in *C. lefebvrei*, probabilmente perché è l'unica delle tre specie che si arrampica sugli alberi, e nell'area delle cornee e numero di ommatidi, maggiore in *C. coriaceus*, specie che predilige habitat aperti.

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