

Shared allometric trajectories but contrasting sexual size dimorphism in *Osmoderma barnabita* and *Rosalia alpina* from the Eastern Carpathians, Romania

Marian D. Mirea^{1,2}, Iulia V. Miu¹, Lavinia C. Pindaru^{1,2}, Steluta Manolache¹, Laurentiu Rozylowicz¹

¹ University of Bucharest, Center for Environmental Research, I. N. Balcescu, Bucharest 010041, Romania

² Doctoral School in Geography Simion Mehedinti - Nature and Sustainable Development, University of Bucharest, Bucharest 010041, Romania

<https://zoobank.org/27318808-9F92-49CB-B218-A1F1844E8653>

Corresponding author: Marian D. Mirea (dumitru-marian.mirea@geo.unibuc.ro)

Academic editor: Serena Magagnoli ♦ Received 4 February 2026 ♦ Accepted 24 April 2026 ♦ Published 7 May 2026

Abstract

Sexual size dimorphism and morphometric variation provide valuable insights into population ecology, habitat quality, and evolutionary processes in insects. However, morphometric data for saproxylic beetles remain limited across much of Europe, particularly in the Carpathian Mountains of Romania, which host some of the largest contiguous forest ecosystems and are a major biodiversity hotspot for these species, despite their high conservation importance. We investigated sexual size dimorphism patterns and allometric relationships in two protected saproxylic beetles, *Osmoderma barnabita* Motschulsky, 1845 (Scarabaeidae) and *Rosalia alpina* Linnaeus, 1758 (Cerambycidae), from the Putna-Vrancea Natural Park, Romania. Between 2022 and 2025, we captured 776 *Osmoderma barnabita* and 268 *Rosalia alpina* individuals using pheromone-baited traps and measured body length, body width, and fresh mass. *Osmoderma barnabita* exhibited weak male-biased sexual size dimorphism, with males slightly larger in body length (+3.4%) and body mass (+5.0%), while body width showed no significant difference between sexes. In contrast, *Rosalia alpina* displayed female-biased sexual size dimorphism across all traits, with the strongest dimorphism in body mass (+13.2%). Standardized Major Axis regression showed positive allometry of body width relative to body length in both species, indicating increased robustness with size. Body mass scaled isometrically with body length, with no sex-specific differences in allometric slopes, suggesting that sexual size dimorphism reflects uniform size shifts along shared developmental trajectories. Linear Discriminant Analysis achieved only moderate classification accuracy (63.5% for *Osmoderma barnabita*; 65.3% for *Rosalia alpina*), reflecting substantial morphological overlap between sexes. These findings establish baseline morphometric data essential for long-term population monitoring and conservation planning in the Eastern Carpathian forests.

Key Words

Baseline data, morphometrics, pheromone trapping, saproxylic beetles, trait scaling

Introduction

Body size and sexual size dimorphism are key traits in insects, integrating genetic, developmental, and environmental influences and providing valuable insights into population status, habitat quality, and ecological functioning (Angilletta 2004; Chown and Gaston 2010; Fountain & Jones et al. 2015; Moretti et al. 2017;

Beukeboom 2018; Ferracini et al. 2025; Cardoso et al. 2026). Sexual size dimorphism arises from the interplay of natural and sexual selection acting differently on males and females (Blanckenhorn 2005; Stillwell et al. 2010). In most insect species, sexual size dimorphism is female-biased, as fecundity selection favors larger females capable of producing and carrying more eggs (Budečević et al. 2021; Zhu et al. 2025). Male-biased sexual size

dimorphism is relatively uncommon and is generally seen as a derived condition linked to intense sexual selection via same-sex competition or female choice (Andersson and Iwasa 1996; Pomfret and Knell 2006; Blanckenhorn et al. 2007).

Coleoptera, one of the most diverse insect orders, presents substantial variation in sexual size dimorphism, ranging from inconspicuous to extreme dimorphism (Kawano 2006; Bouchard et al. 2017). Female-biased sexual size dimorphism predominates in beetles, reflecting the strong link between female body size and reproductive output (Teder and Tammaru 2005; Torres-Vila 2017). However, male-biased sexual size dimorphism occurs in several lineages where larger males or exaggerated traits such as enlarged mandibles, horns, or elongated antennae provide advantages in mating competition or mate searching (Andersson and Iwasa 1996; Hanks 1999; Romiti et al. 2015; Weber et al. 2023; Luiselli et al. 2025). In longhorn beetles (Cerambycidae), larger females generally show higher fecundity, while larger males often benefit from increased longevity, mating opportunities, and sensory efficiency (Lu et al. 2013; Torres-Vila et al. 2016; Torres-Vila 2017). Although sexual size dimorphism is often assumed to be species-specific, its magnitude can vary markedly among populations, across environmental gradients, and between years (Songvorawit et al. 2019; Sukhodolskaya et al. 2020; Ferracini et al. 2025; Luiselli et al. 2025).

The diversity of dimorphism in insects is also explained by sex-specific phenotypic plasticity, with female body size frequently being more sensitive to environmental conditions such as resource availability and habitat quality (Stillwell et al. 2010; Rohner et al. 2018; Toh et al. 2022; Cordeschi et al. 2024). In beetles, particularly xylophagous and saproxylic species, adult body size is strongly shaped by larval resource availability, host characteristics, dead-wood quantity, old-growth tree presence, tree diversity, and light conditions (Michalcewicz and Ciach 2012; Ciach and Michalcewicz 2013; Lupi et al. 2015; Torres-Vila et al. 2018; Lindman et al. 2023). Consequently, morphometric traits and sexual size dimorphism provide a powerful and practical framework for linking insect ecology, evolutionary processes, and conservation-relevant population responses to environmental change (Chown and Gaston 2010; Kiritani 2013; Torres-Vila et al. 2017; Tseng et al. 2018; Hagge et al. 2021).

The saproxylic beetles *Osmoderma barnabita* Motschulsky, 1845 (Coleoptera: Scarabaeidae) and *Rosalia alpina* Linnaeus, 1758 (Coleoptera: Cerambycidae) represent complementary models for studying sexual size dimorphism in forest-dependent insects. *Rosalia alpina* exhibits clear sexual dimorphism, most notably in antennal length, a trait linked to mate detection and sexual selection in longhorn beetles (Michalcewicz and Ciach 2012; Campanaro et al. 2017), whereas *Osmoderma barnabita* shows only weak external sexual differentiation and lacks conspicuous secondary sexual traits (Svensson et al. 2011; Maurizi et al. 2017). This contrast enables comparative analyses of how sexual selection and ecological constraints shape sexual size dimorphism across taxa with

different life-history strategies. While studies on *Rosalia alpina* have primarily focused on sexually dimorphic appendages (Campanaro et al. 2017; Rossi De Gasperis et al. 2017), incorporating general morphometric traits such as body length, body width, and mass may provide additional insights into sex-specific growth patterns and the ecological drivers of sexual size dimorphism (Dubois et al. 2010; Michalcewicz and Ciach 2012; Ciach and Michalcewicz 2013).

In many saproxylic beetles, sexual dimorphism in external morphology is subtle, resulting in substantial overlap between males and females for most morphometric traits (Hedin and Ranius 2002; Svensson et al. 2011; Lindman et al. 2023). In *Osmoderma barnabita*, distinguishing sexes based on external features is particularly difficult, as differences are generally limited to minor size-related variation (Maurizi et al. 2017; Lindman et al. 2023). This pattern likely reflects the combined influence of ecological constraints related to larval development in dead wood (Lindman et al. 2023). Consequently, sexual size dimorphism in such species might be mainly expressed through overall body size or mass, rather than through pronounced morphological traits, highlighting the importance of detailed morphometric analyses to understand sex-specific growth and improve population assessments in conservation efforts.

Investigating patterns of sexual size dimorphism and subtle morphological differentiation in saproxylic beetles is particularly important when analyzing species abundance in regions of high conservation value, such as the Eastern Carpathian Mountains, Romania (Mirea et al. 2021; Munteanu et al. 2022; Rozyłowicz et al. 2024), which provide suitable habitats for species of European conservation concern, including *Osmoderma barnabita* and *Rosalia alpina* (Nieto and Alexander 2010). However, past forestry management practices, such as selective logging and the systematic removal of veteran trees, have simplified forest structure and caused sharp declines in saproxylic insect communities (Brodie et al. 2019). As a result, many saproxylic species now occur in a limited number of forest stands, often fragmented and isolated from larger, high-quality old-growth forest populations, despite their broader potential distribution (Miu et al. 2020; Mirea et al. 2024). Given the high conservation value of the Eastern Carpathian Mountains and the limited availability of detailed morphometric data for saproxylic beetles in this region, this study aims to provide a focused assessment of sexual size dimorphism and morphological variation in two protected species, *Osmoderma barnabita* and *Rosalia alpina*. By analyzing populations from relatively well-preserved forest habitats, we seek to clarify how subtle morphological differences between sexes are expressed in species with contrasting degrees of sexual dimorphism. Our objectives are: (1) to assess sexual size dimorphism in body size and fresh mass; (2) to evaluate sex-specific allometric scaling of morphometric traits; and (3) to evaluate the potential of external morphometry for sex discrimination in saproxylic beetles. More specifically, we aim to answer the following questions:

Do males and females differ in body size? Do morphometric traits scale isometrically or allometrically with body length, and do these scaling relationships differ between sexes? How accurately can sex be predicted using external morphometric traits?

By answering these research questions, we advance understanding of the ecological and evolutionary drivers of morphological variation in saproxylic beetles and provide practical tools for monitoring and conserving species of European concern.

Methods

Study area

We carried out the analysis in Putna-Vrancea Natural Park (ROSAC0208 Putna-Vrancea), Romania, located in the central and northwestern sectors of the Vrancea Mountains (Eastern Romanian Carpathians). Putna-Vrancea Natural Park was established in 2004 by Government Decision 2151 regarding establishing the protected natural area regime, while the Natura 2000 statue was awarded in 2022 (MMAP 2026). Land cover is currently characterized by extensive forested areas, including patches of old-growth forests. The dominant species are *Fagus sylvatica*, *Abies alba*, and *Picea abies*, with beech forests dominating the landscape. Alluvial forests of *Alnus glutinosa* and *Fraxinus excelsior* are also present.

Saproxylic beetle surveys

We focused on two saproxylic beetle species of conservation interest: the alpine longhorn beetle *Rosalia alpina* Linnaeus, 1758 (Cerambycidae) and the hermit beetle *Osmoderma barnabita* Motschulsky, 1845 (part of the *Osmoderma eremita* species complex, Scarabaeidae). Beetles were captured between 2022 and 2025 in seven sampling sites within Putna-Vrancea Natural Park using non-lethal windowpane flight intercept traps fitted with a cover and a 0.5-L collection jar (Alpha Scent, Inc., Oregon, USA) (Table 1, Suppl. material 1). Traps were installed at a minimum of 1.5 m height (McLaughlin et al. 2003), and baited with a mix of pheromones (i.e., C6 diol, 3-hydroxy-2-octanone, Fuscumol acetate, Fuscumol, Monochamol, \pm 2-methylbutan-1-ol, Ethanol, Decalactone) provided by Synergy Semiochemicals Corp., BC, Canada. Pheromones were selected to attract the two species analyzed in this article, as well as other protected saproxylic species such as *Cerambyx cerdo* and *Lucanus cervus* (Dunn et al. 2016; Brodie et al. 2019).

Traps were inspected every 3 days to ensure that insects were not harmed, and the beetles were then released several meters away from the trap. Traps were placed at least 50 m apart to reduce spatial autocorrelation and recapture bias, and all individuals were marked with a unique paint code applied to the elytra to ensure reliable individual identification across captures and to prevent

double-counting, enabling subsequent analyses of movement behavior, dispersal, home range and habitat use (Wang 2017; Mirea et al. 2026).

Standardized photographs were taken for each live specimen for subsequent morphometric measurements. Each beetle was photographed with a measurement scale in the frame. To ensure accuracy, the beetle and the scale were placed on the same horizontal plane, and photographs were taken vertically from above with the camera perpendicular to the dorsal surface of the insect. Images were retaken if the beetle was not oriented horizontally, if either the insect or the scale was out of focus, or if the image plane was not parallel to the plane of the specimen and scale. This procedure ensured proper alignment for later measurement. Morphometric measurements were obtained from the photographs using ImageJ (Schneider et al. 2012). The measurement scale was first calibrated within each image, after which body length and maximum body width were recorded. Body length (mm) was measured from the anterior margin of the head, excluding the mandibles, to the elytral apex. Maximum body width (mm) was measured across the widest part of the elytra. Body weight (fresh mass) (g) was measured using a precision (weighing accuracy: 0.01 g) scale. Each set of measurements was linked to the individual's photo ID and field code (Suppl. material 2). Traits such as antennal length were not included in our analyses, as their accurate measurement under field conditions is unreliable. Sex was determined based on species-specific external morphological traits. For *Rosalia alpina*, individuals were sexed using well-established traits of sexual dimorphism, including differences in antennal length and the presence of a visible ovipositor in females (Campanaro et al. 2017). For *Osmoderma barnabita*, sex determination was based on differences in pronotum shape and the morphology of the terminal abdominal segment (pygidium). Males were identified by a more convex pronotum and a large, distinctly convex pygidium. In contrast, females exhibited a more rounded, smaller and less convex pygidium (Maurizi et al. 2017). These features allowed consistent differentiation between sexes during field handling.

Table 1. Geographic coordinates of sampling sites within Putna-Vrancea Natural Park (Romania).

Site name	Site ID	Latitude, Longitude	Elevation (m)	Number of traps	Cumulative trap-days
Babovici	S1	45.92940°N, 26.44988°E	808	20	198
Tunel	S2	45.93779°N, 26.60981°E	737	20	198
Coasa	S3	45.97894°N, 26.59350°E	984	20	198
Galaciuc	S4	45.91615°N, 26.65691°E	677	20	198
Beuca	S5	45.98632°N, 26.45604°E	1295	20	198
Marului	S6	45.96302°N, 26.42168°E	993	20	198
Cucu	S7	45.92119°N, 26.62793°E	625	40	198

Data analysis

To provide an overview of size variation in the population, descriptive statistics were computed across all individuals of both species by sex. We focused on three morphometric traits: body length, body width, and body weight (fresh mass).

Sexual size dimorphism (SSD) was quantified using the Sexual Dimorphism Index (SDI), calculated as $SDI = (\text{mean of the larger sex} / \text{mean of the smaller sex}) - 1$ (Lovich and Gibbons 1992). Positive SDI values indicate female-biased dimorphism, while negative values indicate male-biased dimorphism (Fairbairn 1997). To test for sex differences in morphometric traits, we used non-parametric Mann-Whitney U (Wilcoxon rank-sum) tests for body length, body width, and fresh mass (Zar 2010).

To determine whether the morphometric traits scale isometrically or allometrically with body length, and whether scaling patterns differ between sexes, we used Standardized Major Axis (SMA) regression on log-transformed data. SMA regression is appropriate when both variables are measured with errors, and there is no clear distinction between dependent/independent variables, as is typically the case in allometric studies, where neither variable can be considered a predictor (Warton et al. 2006). Slopes were tested against isometric expectations ($b = 1$ for linear measurements; $b = 3$ for mass-length relationships, following the cubic relationship between mass and linear dimensions) using one-sample tests implemented in the *smart R* package (Warton et al. 2012; R Core Team 2024), based on 95% confidence intervals and likelihood ratio tests. Sex-specific differences in allometric slopes were assessed using likelihood ratio tests. When slopes were homogeneous between sexes ($p > 0.05$), we tested for differences in elevation (intercept) to determine whether the sexes differed in mean trait size at a common body length (Warton et al. 2006).

To evaluate the discriminatory power of morphometric traits for sex identification, we performed Linear Discriminant Analysis (LDA) using the *MASS R* package (Venables and Ripley 2002; R Core Team 2024). Classification accuracy was assessed using leave-one-out cross-validation, which provides a nearly unbiased estimate of the true error rate by iteratively classifying each observation using a discriminant function derived from all other observations (Lachenbruch and Mickey 1968). In LDA, prior probabilities represent the expected class frequencies before examining measurements, influencing how the classifier assigns observations. Our sample exhibited a female-biased sex ratio for *Osmoderma barnabita*, whereas for *Rosalia alpina* the sex ratio was approximately balanced. The female-biased sample in *Osmoderma barnabita* likely reflects pheromone-based trapping and sex-specific dispersal rather than true population structure (Larsson et al. 2003; Dubois et al. 2010; Svensson et al. 2011). Thus, we specified equal prior probabilities (0.5, 0.5) based on the general expectation of balanced primary sex ratios in saproxylic beetles. For *Rosalia alpina*, where sex ratios were approximately

balanced, priors had minimal influence. This approach ensured methodological consistency across species. Multicollinearity among predictors was evaluated using Variance Inflation Factors (VIF). Graphs were created using *ggplot R* package (Wickham 2016; R Core Team 2024).

Results

Osmoderma barnabita

Sexual size dimorphism. A total of 776 *Osmoderma barnabita* individuals were captured and measured between 2022 and 2025. The sample included 558 females (71.9%) and 218 males (28.1%), reflecting a female-biased sex ratio typical of pheromone-baited trap captures for this species. Males differed significantly from females in body length (males: 3.25 ± 0.23 cm; females: 3.14 ± 0.24 cm; Mann-Whitney $U = 45.342$, $p < 0.001$) and body weight (males: 1.76 ± 0.37 g; females: 1.68 ± 0.41 g; Mann-Whitney $U = 52.336$, $p = 0.002$). In contrast, no significant difference between sexes was observed in body width (males: 1.71 ± 0.14 cm; females: 1.69 ± 0.15 cm; Mann-Whitney $U = 55.797$, $p = 0.073$) (Fig. 1).

Negative SDI values confirmed that males were larger across most traits, with the strongest dimorphism in body weight (SDI = -0.050), followed by body length (SDI = -0.034). Body width showed the weakest dimorphism (SDI = -0.012), consistent with the statically non-significant differences between sexes.

Allometric relationships. Standardized Major Axis (SMA) regression revealed contrasting allometric patterns between width-length and weight-length relationships (Fig. 2). Width exhibited positive allometry relative to length ($b = 1.133$, 95% CI: 1.090–1.177, $R^2 = 0.704$), with the slope significantly exceeding isometric expectations ($b = 1$; $p < 0.001$), indicating disproportionate increases in body width with size. In contrast, weight scaled isometrically with length ($b = 3.142$, 95% CI: 2.975–3.317, $R^2 = 0.404$), with no significant deviation from the expected cubic relationship ($b = 3$; $p = 0.097$). Sex-specific analyses showed no significant differences in slopes or elevations between males and females for either relationship, indicating shared allometric trajectories across sexes.

Sex discrimination. Linear Discriminant Analysis (LDA) using log-transformed morphometric variables achieved moderate classification accuracy for sex identification. Using equal prior probabilities (0.5, 0.5) to account for trapping-induced sampling bias, leave-one-out cross-validation yielded an overall classification accuracy of 63.5%, with sensitivity (correct male identification) of 64.7% and specificity (correct female identification) of 63.1%. Variance Inflation Factors among predictors (1.78–3.60) were below thresholds indicating multicollinearity ($VIF < 5$).

The linear discriminant function was primarily weighted by body length (coefficient: 54.2) and body width (coefficient: -35.3), with body weight contributing minimally (coefficient: 0.88). The distribution of LD1

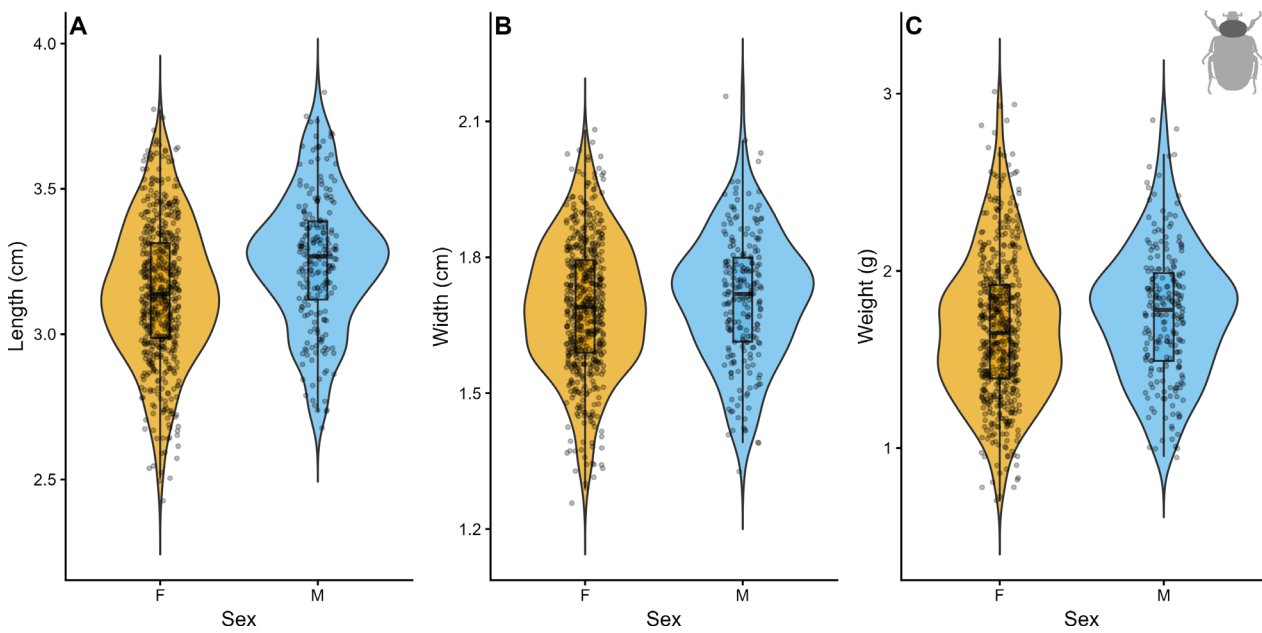


Figure 1. Violin plots of morphometric traits by sex in *Osmoderma barnabita*. **A.** Body length; **B.** Body width; **C.** Body weight (fresh mass). Individual data points are shown as jittered dots.

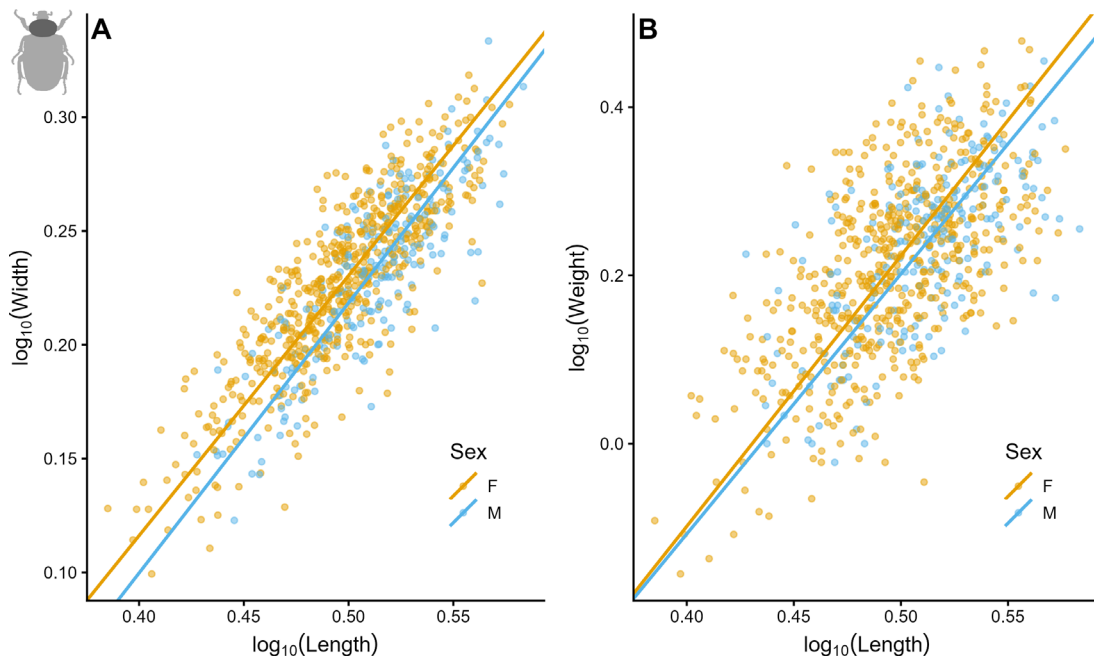


Figure 2. Allometric relationships between \log_{10} -transformed morphometric variables in *Osmoderma barnabita*. **A.** Width-length relationship showing positive allometry (slope = 1.133); **B.** Weight-length relationship showing isometric scaling (slope = 3.142). Regression lines are shown separately for each sex.

scores (Fig. 3) showed substantial overlap between sexes, consistent with the moderate classification accuracy.

Rosalia alpina

Sexual size dimorphism. A total of 268 *Rosalia alpina* individuals were captured and measured during the study period (2022–2025). The sample included 120 females (44.8%) and 148 males (55.2%), reflecting a slightly male-biased sex ratio. Females were significantly larger than males across all measured traits: body length (females: 2.78 ± 0.32 cm; males: 2.62 ± 0.32 cm;

Mann-Whitney $U = 11.386$, $p < 0.001$), body width (females: 0.70 ± 0.08 cm; males: 0.64 ± 0.08 cm; Mann-Whitney $U = 12.258$, $p < 0.001$), and body weight (females: 0.42 ± 0.15 g; males: 0.38 ± 0.14 g; Mann-Whitney $U = 10.546$, $p = 0.008$) (Fig. 4).

Positive SDI values confirmed female-biased sexual size dimorphism across all traits, with the strongest dimorphism in body weight (SDI = +0.132), followed by body width (SDI = +0.091) and body length (SDI = +0.060).

Allometric relationships. Standardized Major Axis (SMA) regression indicated that body width increased allometrically with body length in *Rosalia alpina* (Fig. 5).

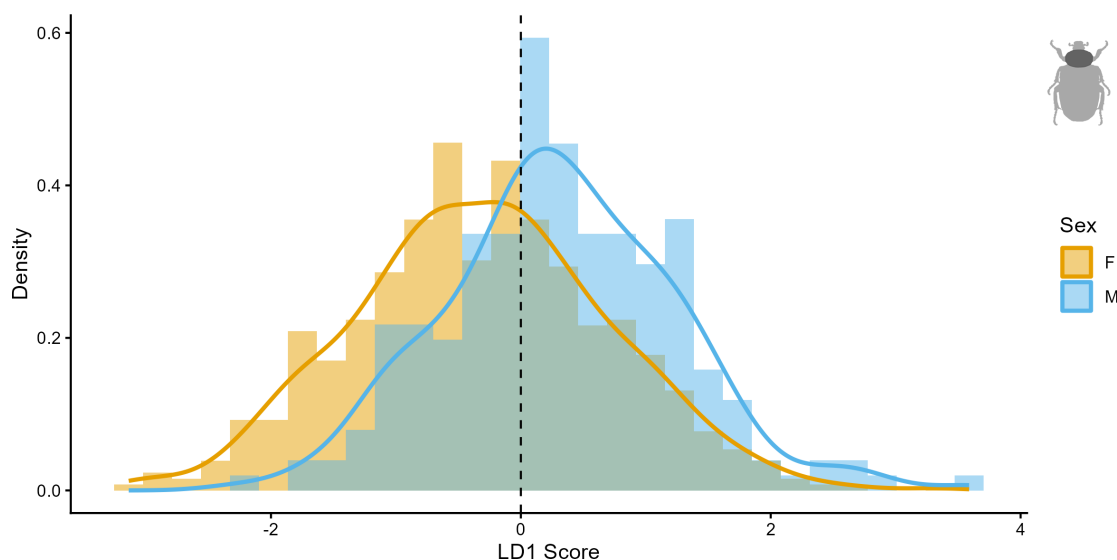


Figure 3. Distribution of Linear Discriminant Analysis (LDA) scores by sex in *Osmoderma barnabita*. The dashed vertical line indicates the classification boundary (LD1 = 0). Histograms show frequency distributions with overlaid density curves.

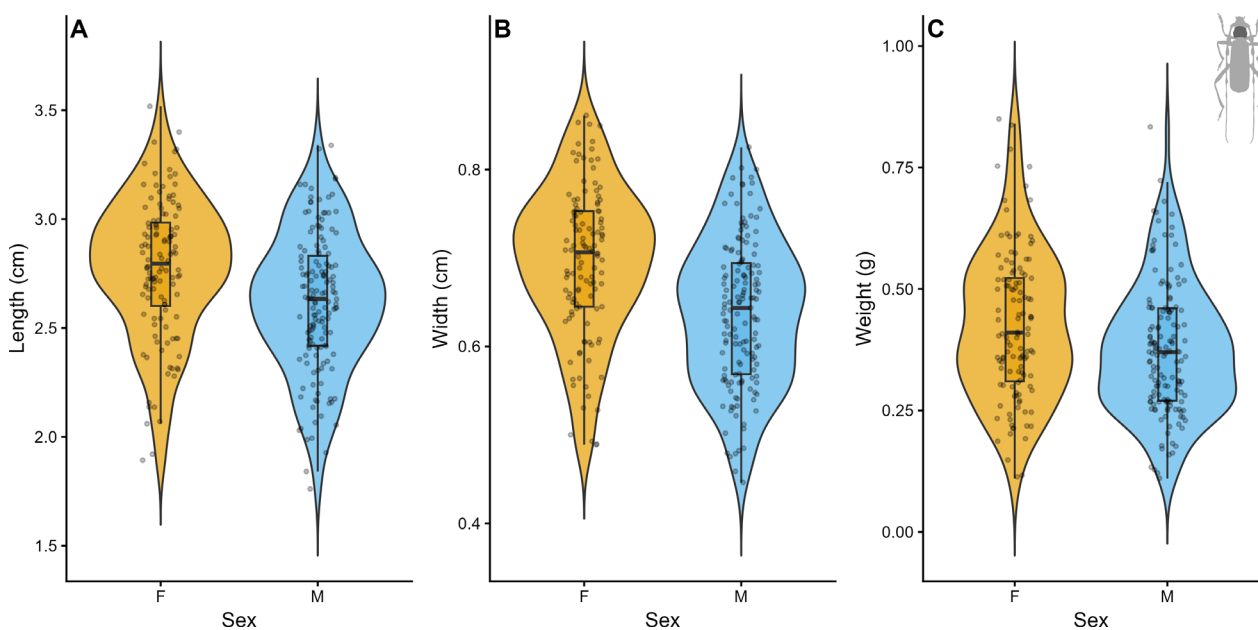


Figure 4. Violin plots of morphometric traits by sex in *Rosalia alpina*. **A.** Body length; **B.** Body width; **C.** Body weight (fresh mass). Individual data points are shown as jittered dots.

Width exhibited positive allometry relative to length ($b = 1.081$, 95% CI: 1.025–1.139, $R^2 = 0.811$), with the slope significantly exceeding isometric expectations ($b = 1$; $p = 0.004$). Weight scaled isometrically with length ($b = 3.070$, 95% CI: 2.860–3.296, $R^2 = 0.653$), with no significant deviation from the expected cubic relationship ($b = 3$; $p = 0.523$). Sex-specific analyses showed no significant differences in slopes or elevations between males and females for either relationship, indicating shared allometric trajectories across sexes.

Sex discrimination. Linear Discriminant Analysis (LDA) using log-transformed morphometric variables achieved moderate classification accuracy for sex identification. Using equal prior probabilities (0.5, 0.5),

leave-one-out cross-validation yielded an overall classification accuracy of 65.3%, with sensitivity (correct male identification) of 62.8% and specificity (correct female identification) of 68.3%. Variance Inflation Factors among predictors ranged from 2.97 to 6.36. The elevated VIF for body length (6.36) indicates moderate multicollinearity with body width.

The linear discriminant function was primarily weighted by body width (coefficient: -31.2), with body length (coefficient: 10.3) and body weight (coefficient: 3.0) contributing less substantially. The distribution of LD1 scores (Fig. 6) showed considerable overlap between sexes, consistent with the moderate classification accuracy.

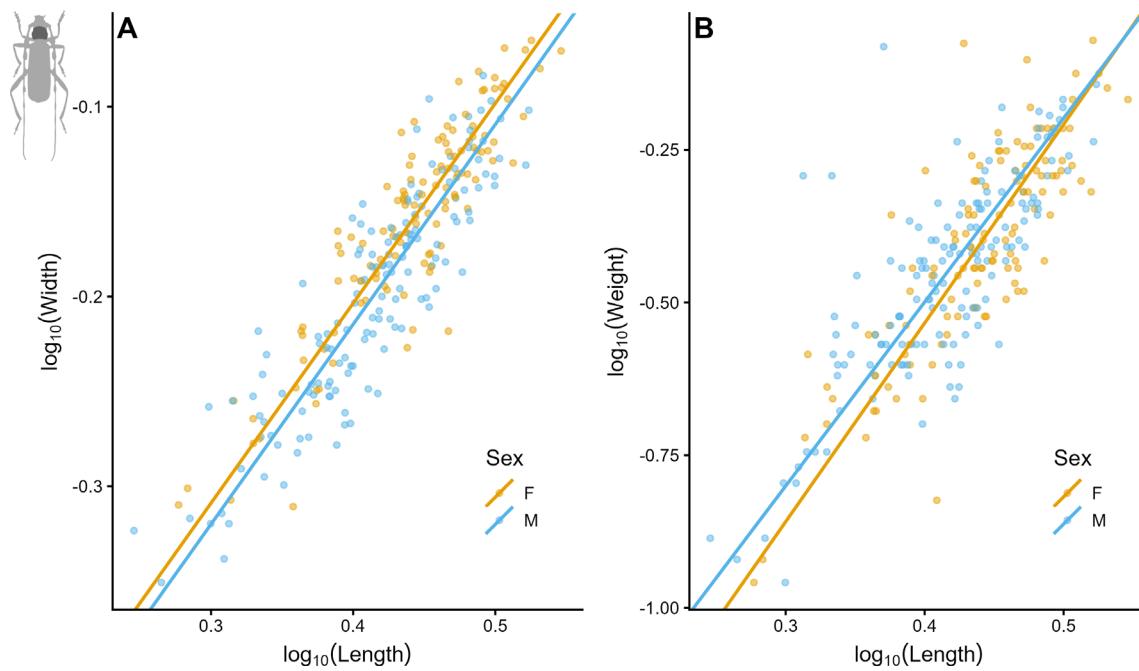


Figure 5. Allometric relationships between \log_{10} -transformed morphometric variables in *Rosalia alpina*. **A.** Width-length relationship showing positive allometry (slope = 1.081); **B.** Weight-length relationship showing isometric scaling (slope = 3.070). Regression lines are shown separately for each sex.

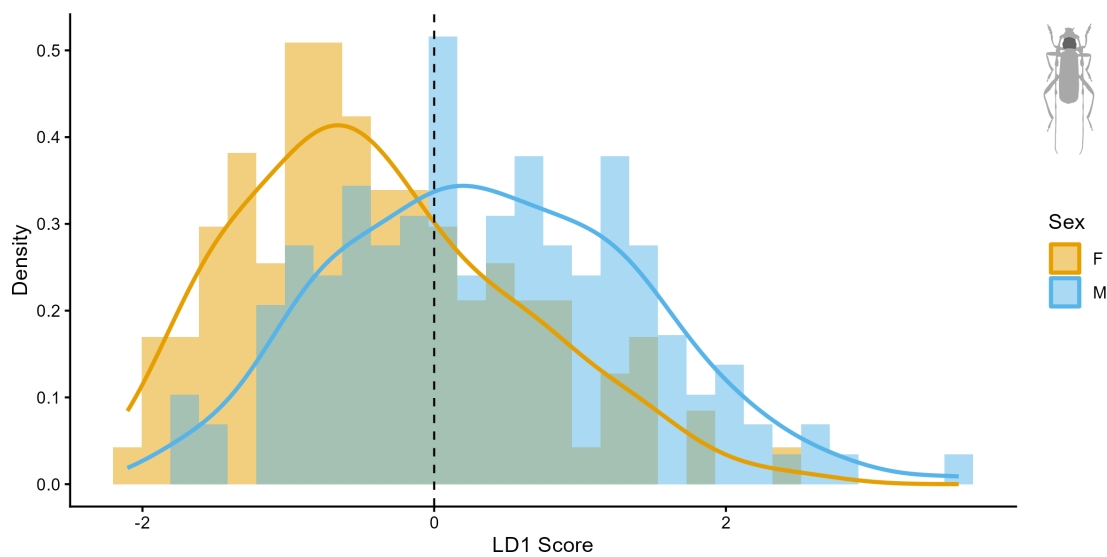


Figure 6. Distribution of Linear Discriminant Analysis (LDA) scores by sex in *Rosalia alpina*. The dashed vertical line indicates the classification boundary (LD1 = 0). Histograms show frequency distributions with overlaid density curves.

Discussion

This study provides the first assessment of sexual size dimorphism and morphometric variation in two protected saproxylic beetles, *Osmoderma barnabita* (Scarabaeidae) and *Rosalia alpina* (Cerambycidae), from the Eastern Carpathian Mountains of Romania. Morphometric studies of genus *Osmoderma* are rare in the peer-reviewed literature, with quantitative body size data most often reported as secondary information within ecological, conservation, or dispersal-focused studies rather than systematic morphometric investigations (Ranius and Hedin 2001; Ulrich 2007; Svensson et al. 2011; Lindman et al. 2023). Within

this limited framework, Maurizi et al., (2017) have shown that sexual differences within the *Osmoderma barnabita* are less pronounced than those observed in the *Osmoderma eremita*. This pattern is consistent with our findings, which reveal weak sexual size dimorphism and substantial morphological overlap between males and females of *Osmoderma barnabita*.

Our results indicate that *Osmoderma barnabita* males are slightly larger than females in body length (+3.4%) and body mass (+5.0%), whereas no significant sex-related differences were detected in body width. Consequently, sexual size dimorphism is male-biased but of low magnitude, as reflected by SDI values close to zero.

Although female-biased SSD predominates across most insect taxa, weak male-biased dimorphism is a characteristic pattern within Cetoniinae beetles, being linked to the intensity of male-male competition, even in the absence of exaggerated secondary sexual traits (Dubois et al. 2010; Svensson et al. 2011; Vendl et al. 2016, 2018).

The weak male-biased SSD observed in *Osmoderma barnabita* individuals may be related to the high quality and stability of their developmental microhabitats. In old-growth forests, large hollow trees can provide nutrient-rich larval substrates that potentially reduce developmental constraints and limit sex-specific divergence in growth patterns (Ranius and Hedin 2001; Sverdrup-Thygeson et al. 2010). At the same time, larger body size may still confer advantages in both sexes, being associated with higher fecundity in females and potentially increased mating success in males (Toh et al. 2022). Our allometric analyses further support this result. Positive allometry in body width indicates that larger individuals are proportionally more robust, suggesting that high habitat quality not only allows increased body size but also promotes structural investment, potentially linked to reproductive performance or survival (Emlen and Nijhout 2000; Vendl et al. 2016). In contrast, the isometric relationship between body mass and body length indicates that individuals maintain consistent body proportions and tissue density across size classes, without becoming disproportionately heavier or lighter as size increases. This pattern is consistent with findings reported for *Holotrichia oblita* (Scarabaeidae) by Zhu et al., (2025). Importantly, males and females exhibited identical allometric scaling relationships, characterized by similar slopes and intercepts. This indicates that sexual size dimorphism in *Osmoderma barnabita* arises from a uniform size shift along a shared allometric trajectory rather than from sex-specific differences in the scaling of body dimensions.

The LDA analysis indicated substantial overlap between male and female morphometric distributions in our individuals. This pattern is predicted by mating systems theory: when sexual selection operates primarily on non-morphological traits (pheromone quality, behavioral displays), body size distributions tend to converge between sexes (Larsson et al. 2003; Blanckenhorn 2005; Kawano 2006; Kishi et al. 2015). In contrast to the weak male-biased dimorphism observed in *Osmoderma barnabita*, *Rosalia alpina* exhibits a markedly different, female-biased pattern of sexual size dimorphism, consistent with family-level differences in which fecundity selection favors larger female body size.

Analysis of SSD in *Rosalia alpina* indicates that females are significantly larger than males across all examined traits, with the strongest dimorphism expressed in body mass (+13.2%). This pattern is consistent with the findings of Michalcewicz and Ciach (2012), who reported a statistically significant female-biased difference of approximately 10% in elytron length. Female-biased SSD in insects is often interpreted as a consequence of fecundity selection, whereby larger females may achieve

higher reproductive output through increased egg number or size. In *Rosalia alpina*, the observed female-biased SSD is consistent with this general pattern; however, as reproductive output was not directly measured in this study, this explanation should be considered a plausible interpretation rather than a demonstrated mechanism. Additionally, such patterns are widespread among Cerambycidae and may also be shaped by variation in the quantity and quality of larval food resources (Teder and Tammaru 2005; Kawano 2006; Stillwell et al. 2010; Torres-Vila 2017; Rossi De Gasperis et al. 2018). Accordingly, our results align well with documented SSD patterns across multiple cerambycid species (Rossi De Gasperis et al. 2018; Torres-Vila et al. 2018).

To our knowledge, no studies have reported body mass data for *Rosalia alpina*, making our study a novel contribution that fills a gap in the species' morphometric literature. Existing reference works, including the standardized monitoring guidelines of Campanaro et al., (2017), compile adult body length and maximum body width from multiple sources, but do not include weight data.

Allometric analyses revealed that body width in *Rosalia alpina* increases disproportionately with body length, indicating positive allometry and a progressive increase in body robustness with increasing size. This represents a further novel contribution to the morphometric characterization of the species. In contrast, body mass scaled isometrically with body length, suggesting that individuals maintain consistent body proportions and tissue density across size classes. Importantly, no sex-specific differences were detected in either slope or elevation for these relationships, indicating that males and females share a common allometric trajectory and that SSD arises from a uniform size shift rather than sex-specific scaling of body dimensions.

The observed isometric mass-length scaling, with an exponent close to 3.0, is strongly supported by the comprehensive beetle allometry study of Zhu et al. (2025), who have found that the 95% confidence intervals for mass-length scaling included 3 in both sexes of *Holotrichia oblita* (Scarabaeidae). Notably, Zhu et al. (2025) have also reported no sex-specific differences in scaling exponents despite females being significantly heavier and experiencing greater wing loading, a pattern that closely parallels our findings for *Rosalia alpina*.

Finally, Linear Discriminant Analysis based on external morphometric traits achieved only moderate accuracy (65%) in sex classification, reflecting substantial morphological overlap between males and females. Body width contributed most strongly to discrimination, whereas body length and body mass played a lesser role. The pronounced overlap in discriminant scores, together with moderate multicollinearity among predictors, indicates that sexual dimorphism in external body dimensions is weak. Consequently, morphometric measurements alone, excluding sexually diagnostic traits such as antennae length, are insufficient for reliable sex identification in *Rosalia alpina*.

Morphometric findings connect to conservation through several mechanisms, as they reflect the environmental conditions experienced during development. In saproxylic insects, larval traits are influenced by the quality and availability of the substrate in which they develop (Michalcewicz and Ciach 2012), while both microclimatic conditions and suitability of microhabitats may further shape developmental outcomes (Landvik et al. 2016; Lindman et al. 2023).

By quantifying these patterns, we establish baseline morphometric data on adult body size and sexual size dimorphism for two protected saproxylic beetle species from the Eastern Carpathian Mountains, a hotspot for saproxylic insects. Such data are essential for long-term population monitoring, detecting morphological and demographic responses to environmental change, and informing evidence-based conservation and forest management strategies. Understanding the ecological and evolutionary factors shaping sexual size dimorphism and associated traits is particularly important for species such as *Osmoderma barnabita* and *Rosalia alpina*, which are strongly dependent on old-growth forest and face ongoing threats across much of their distribution (Nieto and Alexander 2010; Seibold et al. 2015). Consequently, the conservation of forest ecosystems is likely crucial for sustaining viable beetle populations and for maintaining natural patterns of morphological variation.

Acknowledgement

The study was supported by LIFE19 NAT/RO/000023 Conservation of saproxylic beetles in the Carpathians LIFE ROSalia (2020–2026). Fieldwork was approved by the Romanian Ministry of Environment, Water, and Forests (Ministry Order 807/May 19, 2021).

References

- Andersson M, Iwasa Y (1996) Sexual selection. *Trends in Ecology & Evolution* 11: 53–58. [https://doi.org/10.1016/0169-5347\(96\)81042-1](https://doi.org/10.1016/0169-5347(96)81042-1)
- Angilletta MJ (2004) Temperature, growth rate, and body size in ectotherms: Fitting pieces of a life-history puzzle. *Integrative and Comparative Biology* 44: 498–509. <https://doi.org/10.1093/icb/44.6.498>
- Beukeboom LW (2018) Size matters in insects – an introduction. *Entomologia Experimentalis et Applicata* 166: 2–3. <https://doi.org/10.1111/eea.12646>
- Blanckenhorn WU (2005) Behavioral causes and consequences of sexual size dimorphism. *Ethology* 111: 977–1016. <https://doi.org/10.1111/j.1439-0310.2005.01147.x>
- Blanckenhorn WU, Meier R, Teder T (2007) Rensch's rule in insects: patterns among and within species. In: Fairbairn DJ, Blanckenhorn WU, Székely T (Eds) *Sex, Size and Gender Roles*. Oxford University Press/Oxford, 60–70. <https://doi.org/10.1093/acprof:oso/9780199208784.003.0007>
- Bouchard P, Smith ABT, Douglas H, Gimmel ML, Brunke AJ, Kanda K (2017) Biodiversity of Coleoptera. In: Footitt RG, Adler PH (Eds) *Insect Biodiversity*. Wiley, 337–417. <https://doi.org/10.1002/9781118945568.ch11>
- Brodie BS, Popescu VD, Iosif R, Ciocanea C, Manolache S, Vanau G, Gavrilidis AA, Serafim R, Rozyłowicz L (2019) Non-lethal monitoring of longicorn beetle communities using generic pheromone lures and occupancy models. *Ecological Indicators* 101: 330–340. <https://doi.org/10.1016/j.ecolind.2019.01.038>
- Budečević S, Savković U, Đorđević M, Vlajnić L, Stojković B (2021) Sexual dimorphism and morphological modularity in *Acanthoscelides obtectus* (Say, 1831) (Coleoptera: Chrysomelidae): A Geometric Morphometric Approach. *Insects* 12: 350. <https://doi.org/10.3390/insects12040350>
- Campanaro A, Redolfi De Zan L, Hardersen S, Antonini G, Chiari S, Cini A, Mancini E, Mosconi F, Rossi De Gasperis S, Solano E, Bologna MA, Sabbatini Peverieri G (2017) Guidelines for the monitoring of *Rosalia alpina*. *Nature Conservation* 20: 165–203. <https://doi.org/10.3897/natureconservation.20.12728>
- Cardoso P, Baker NJ, Boieiro M, Bonte D, Borges PAV, Braby MF, Branco V, Chobanov D, Correia L, Dalton DT, Damas Mora M, Didham RK, Forster L, Glatz R, Gorneau JA, Hochkirch A, Kirse A, Lichtenberg EM, Macías Hernández N, Miličić M, Moir M, Moreno García P, Neessen R, Noriega JA, Penick CA, Perry KI, Pryke J, Rego C, Roeder KA, Saussure S, Shirey V, Sihvonen P, Svetnik I, Tarasov S, Trindade P, Welti EAR, Wong M, Scherber C (2026) Toward a global repository of insect traits (GRIT). *Insect Conservation and Diversity* 19: 253–267. <https://doi.org/10.1111/icad.70035>
- Chown SL, Gaston KJ (2010) Body size variation in insects: a macroecological perspective. *Biological Reviews* 85: 139–169. <https://doi.org/10.1111/j.1469-185X.2009.00097.x>
- Ciach M, Michalcewicz J (2013) Correlation between selected biometric traits of adult *Rosalia alpina* (L.) (Coleoptera: Cerambycidae) and size of their exit holes: New perspectives on insect studies? *Polish Journal of Ecology* 61: 349–355. <https://doi.org/10.2478/v10200-012-0019-6>
- Cordeschi G, Canestrelli D, Porretta D (2024) Sex-biased phenotypic plasticity affects sexual dimorphism patterns under changing environmental conditions. *Scientific Reports* 14: 892. <https://doi.org/10.1038/s41598-024-51204-6>
- Dubois GF, Le Gouar PJ, Delettre YR, Brustel H, Vernon P (2010) Sex-biased and body condition dependent dispersal capacity in the endangered saproxylic beetle *Osmoderma eremita* (Coleoptera: Cetonidae). *Journal of Insect Conservation* 14: 679–687. <https://doi.org/10.1007/s10841-010-9296-0>
- Dunn E, Hough-Goldstein J, Hanks LM, Millar JG, D'Amico V (2016) Range of attraction of pheromone lures and dispersal behavior of cerambycid beetles. *Annals of the Entomological Society of America* 109: 872–880. <https://doi.org/10.1093/aesa/saw055>
- Emlen DJ, Nijhout HF (2000) The development and evolution of exaggerated morphologies in insects. *Annual Review of Entomology* 45: 661–708. <https://doi.org/10.1146/annurev.ento.45.1.661>
- Fairbairn D (1997) Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. *Annual Review of Ecology and Systematics* 28: 659–687. <https://doi.org/10.1146/annurev.ecolsys.28.1.659>
- Ferracini C, Busato E, Alexanov V, Solodovnikov IA, Teofilova T, Langraf V, Borisovskiy A, Luzyanin S, Ruchin A, Stočes D, Anciferov AL, Gorbunov RP, Sukhodolskaya RA (2025) Sexual size dimorphism depends drastically on environment: The case study in ground beetles. *Insects* 16: 1249. <https://doi.org/10.3390/insects16121249>

- Fountain Jones NM, Baker SC, Jordan GJ (2015) Moving beyond the guild concept: developing a practical functional trait framework for terrestrial beetles. *Ecological Entomology* 40: 1–13. <https://doi.org/10.1111/een.12158>
- Hagge J, Müller J, Birkemoe T, Buse J, Christensen RHB, Gossner MM, Gruppe A, Heibl C, Jarzabek Müller A, Seibold S, Siitonen J, Soutinho JG, Sverdrup Thygeson A, Thorn S, Drag L (2021) What does a threatened saproxylic beetle look like? Modelling extinction risk using a new morphological trait database. *Journal of Animal Ecology* 90: 1934–1947. <https://doi.org/10.1111/1365-2656.13512>
- Hanks LM (1999) Influence of the larval host plant on reproductive strategies of cerambycid beetles. *Annual Review of Entomology* 44: 483–505. <https://doi.org/10.1146/annurev.ento.44.1.483>
- Hedin J, Ranius T (2002) Using radio telemetry to study dispersal of the beetle *Osmoderma eremita*, an inhabitant of tree hollows. *Computers and Electronics in Agriculture* 35: 171–180. [https://doi.org/10.1016/S0168-1699\(02\)00017-0](https://doi.org/10.1016/S0168-1699(02)00017-0)
- Kawano K (2006) Sexual dimorphism and the making of oversized male characters in beetles (Coleoptera). *Annals of the Entomological Society of America* 99: 327–341. [https://doi.org/10.1603/0013-8746\(2006\)099\[0327:sdatmo\]2.0.co;2](https://doi.org/10.1603/0013-8746(2006)099[0327:sdatmo]2.0.co;2)
- Kiritani K (2013) Different effects of climate change on the population dynamics of insects. *Applied Entomology and Zoology* 48: 97–104. <https://doi.org/10.1007/s13355-012-0158-y>
- Kishi S, Takakura K, Nishida T (2015) Sexual shape dimorphism accelerated by male–male competition, but not prevented by sex-indiscriminate parental care in dung beetles (Scarabaeidae). *Ecology and Evolution* 5: 2754–2761. <https://doi.org/10.1002/ece3.1558>
- Lachenbruch PA, Mickey MR (1968) Estimation of error rates in discriminant analysis. *Technometrics* 10: 1–11. <https://doi.org/10.1080/00401706.1968.10490530>
- Landvik M, Niemelä P, Roslin T (2016) Opportunistic habitat use by *Osmoderma barnabita* (Coleoptera: Scarabaeidae), a saproxylic beetle dependent on tree cavities. *Insect Conservation and Diversity* 9: 38–48. <https://doi.org/10.1111/icad.12141>
- Larsson MC, Hedin J, Svensson GP, Tolasch T, Francke W (2003) Characteristic odor of *Osmoderma eremita* identified as a male-released pheromone. *Journal of Chemical Ecology* 29: 575–587. <https://doi.org/10.1023/A:1022850704500>
- Landman L, Öckinger E, Ranius T (2023) Microclimate in hollow trees and how it affects an inhabiting beetle species, *Osmoderma eremita*. *Ecological Entomology* 48: 112–126. <https://doi.org/10.1111/een.13206>
- Lovich JE, Gibbons JW (1992) A review of techniques for quantifying sexual size dimorphism. *Growth Dev Aging* 56: 269–281. *Growth, development, and aging: GDA* 56: 269–81.
- Lu W, Wang Q, Tian M, Xu J, Lv J, Qin A (2013) Mating behavior and sexual selection in a polygamous beetle. *Current Zoology* 59: 257–264. <https://doi.org/10.1093/czoolo/59.2.257>
- Luiselli L, Rugiero L, Luiselli R, Amori G, Dendi D, Fa JE (2025) Size matters: exploring sexual size dimorphism and mandible length in stag beetles across tree-size gradients in central Italy. *Rendiconti Lincei. Scienze Fisiche e Naturali* 36: 337–345. <https://doi.org/10.1007/s12210-025-01303-x>
- Lupi D, Jucker C, Rocco A, Harrison R, Colombo M (2015) Notes on biometric variability in invasive species: the case of *Psacotheta hilaris hilaris*. *Bulletin of Insectology* 68: 135–145.
- Maurizi E, Campanaro A, Chiari S, Maura M, Mosconi F, Sabatelli S, Zauli A, Audisio P, Carpaneto GM (2017) Guidelines for the monitoring of *Osmoderma eremita* and closely related species. *Nature Conservation* 20: 79–128. <https://doi.org/10.3897/natureconservation.20.12658>
- McLaughlin JR, Czokajlo D, Warren JC, Teale SA, Kirsch P (2003) Intercept™ panel trap, modified for monitoring forest Cerambycidae (Coleoptera). In: Fosbroke SLC, Gottschalk KW (Eds) Proceedings of the U.S. Department of Agriculture Interagency Research Forum on Gypsy Moth and Other Invasive Species 2002, General Technical Report NE-300. U.S. Department of Agriculture, Forest Service, Northeastern Research Station, Newtown Square, PA, 69 pp. <https://doi.org/10.2737/ne-gtr-315>
- Michalciewicz J, Ciach M (2012) Biometry of adult rosalia longicorn *Rosalia alpina* (L.) (Coleoptera: Cerambycidae) from the Polish Carpathians: a preliminary study. *Polish Journal of Entomology / Polskie Pismo Entomologiczne* 81: 311–320. <https://doi.org/10.2478/v10200-012-0011-1>
- Mirea M, Manolache S, Pioarca-Ciocanea C, Nita A, Miu I, Popescu V, Brodie B, Dragomir M, Militaru I, Chiriac S, Rozyłowicz L (2021) Conservation of saproxylic beetles in the Carpathians. *Research Ideas and Outcomes* 7: e63874. <https://doi.org/10.3897/rio.7.e63874>
- Mirea MD, Miu IV, Popescu VD, Brodie BS, Chiriac S, Rozyłowicz L (2024) Priority conservation areas for protected saproxylic beetles in Romania under current and future climate scenarios. *Biodiversity and Conservation* 33: 2949–2973. <https://doi.org/10.1007/s10531-024-02898-7>
- Mirea MD, Miu IV, Popescu VD, Pindaru LC, Manolache S, Chiriac S, Rozyłowicz L (2026) Hermit beetle (*Osmoderma barnabita*) habitat selection and movement are shaped by tree microhabitat availability in Eastern Romanian Carpathians. *Insect Conservation and Diversity* 19. <https://doi.org/10.1111/icad.70078>
- Miu IV, Rozyłowicz L, Popescu VD, Anastasiu P (2020) Identification of areas of very high biodiversity value to achieve the EU Biodiversity Strategy for 2030 key commitments. *PeerJ* 8: e10067. <https://doi.org/10.7717/peerj.10067>
- Moretti M, Dias ATC, De Bello F, Altermatt F, Chown SL, Azcárate FM, Bell JR, Fournier B, Hedde M, Hortal J, Ibanez S, Öckinger E, Sousa JP, Ellers J, Berg MP (2017) Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits. *Functional Ecology* 31: 558–567. <https://doi.org/10.1111/1365-2435.12776>
- MMAP [Ministerul Mediului Apelor și Pădurilor] (2026) Natura 2000 Standard Data Form ROSAC0208 Putna Vrancea. <https://natura2000.eea.europa.eu/Natura2000/sdf/#/sdf?site=ROSAC0208> [Accessed on: 2026-4-7]
- Munteanu C, Senf C, Nita MD, Sabatini FM, Oeser J, Seidl R, Kummerle T (2022) Using historical spy satellite photographs and recent remote sensing data to identify high conservation value forests. *Conservation Biology* 36: e13820. <https://doi.org/10.1111/cobi.13820>
- Nieto A, Alexander KNA (2010) The status and conservation of saproxylic beetles in Europe. *Cuadernos de biodiversidad*, 3–10. <https://doi.org/10.14198/cdbio.2010.33.01>
- Pomfret JC, Knell RJ (2006) Sexual selection and horn allometry in the dung beetle *Euoniticellus intermedius*. *Animal Behaviour* 71: 567–576. <https://doi.org/10.1016/j.anbehav.2005.05.023>
- R Core Team (2024) R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. <https://doi.org/10.32614/r.manuals>

- Ranius T, Hedin J (2001) The dispersal rate of a beetle, *Osmoderma eremita*, living in tree hollows. *Oecologia* 126: 363–370. <https://doi.org/10.1007/s004420000529>
- Rohner PT, Teder T, Esperk T, Lüpold S, Blanckenhorn WU (2018) The evolution of male-biased sexual size dimorphism is associated with increased body size plasticity in males. *Functional Ecology* 32: 581–591. <https://doi.org/10.1111/1365-2435.13004>
- Romiti F, Tini M, Redolfi De Zan L, Chiari S, Zauli A, Carpaneto GM (2015) Exaggerated allometric structures in relation to demographic and ecological parameters in *Lucanus cervus* (Coleoptera: Lucanidae): ALLOMETRY IN *Lucanus cervus*. *Journal of Morphology* 276: 1193–1204. <https://doi.org/10.1002/jmor.20411>
- Rossi De Gasperis S, Carpaneto GM, Nigro G, Antonini G, Chiari S, Cini A, Mancini E, Mason F, Mosconi F, Redolfi De Zan L, Roversi PF, Sabbatini Peverieri G, Solano E, Campanaro A (2017) Computer-aided photographic identification of *Rosalia alpina* (Coleoptera: Cerambycidae) applied to a mark-recapture study. *Insect Conservation and Diversity* 10: 54–63. <https://doi.org/10.1111/icad.12199>
- Rossi De Gasperis S, Redolfi De Zan L, Romiti F, Hardersen S, Carpaneto GM (2018) Sexual dimorphism and allometry of secondary sexual character in *Morimus asper* (Coleoptera: Cerambycidae). *Zoomorphology* 137: 119–130. <https://doi.org/10.1007/s00435-017-0380-9>
- Rozylowicz L, Popescu VD, Manolache S, Nita A, Gradinaru SR, Mirea MD, Bancila RI (2024) Occupancy and N-mixture modeling applications in ecology: A bibliometric analysis. *Global Ecology and Conservation* 50: e02838. <https://doi.org/10.1016/j.gecco.2024.e02838>
- Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* 9: 671–675. <https://doi.org/10.1038/nmeth.2089>
- Seibold S, Brandl R, Buse J, Hothorn T, Schmid J, Thorn S, Müller J (2015) Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe. *Conservation Biology* 29: 382–390. <https://doi.org/10.1111/cobi.12427>
- Songvorawit N, Butcher BA, Chaisuekul C (2019) Size does not matter: Same-sex sexual behavior occurred regardless of mandible size in male stag beetle *Aegus chelifera chelifera* (Coleoptera: Lucanidae). *Journal of Insect Behavior* 32: 282–289. <https://doi.org/10.1007/s10905-019-09733-w>
- Stillwell RC, Blanckenhorn WU, Teder T, Davidowitz G, Fox CW (2010) Sex differences in phenotypic plasticity affect variation in sexual size dimorphism in insects: From physiology to evolution. *Annual Review of Entomology* 55: 227–245. <https://doi.org/10.1146/annurev-ento-112408-085500>
- Sukhodolskaya RA, Saveliev AA, Ukhova NL, Vorobyova IG, Solodovnikov IA, Anciferov AL, Gordienko TA, Shagidullin RR, Vavilov DN (2020) Modeling sexual differences of body size variation in ground beetles in geographical gradient (The case study in *Pterostichus oblongpunctatus* Fabricius, 1787). *GSC Biological and Pharmaceutical Sciences* 13: 149–161. <https://doi.org/10.30574/gscbps.2020.13.3.0388>
- Svensson GP, Sahlin U, Brage B, Larsson MC (2011) Should I stay or should I go? Modelling dispersal strategies in saproxylic insects based on pheromone capture and radio telemetry: a case study on the threatened hermit beetle *Osmoderma eremita*. *Biodiversity and Conservation* 20: 2883–2902. <https://doi.org/10.1007/s10531-011-0150-9>
- Sverdrup-Thygeson A, Skarpaas O, Ødegaard F (2010) Hollow oaks and beetle conservation: the significance of the surroundings. *Biodiversity and Conservation* 19: 837–852. <https://doi.org/10.1007/s10531-009-9739-7>
- Teder T, Tammaru T (2005) Sexual size dimorphism within species increases with body size in insects. *Oikos* 108: 321–334. <https://doi.org/10.1111/j.0030-1299.2005.13609.x>
- Toh KX, Yap S, Goh TG, Puniamoorthy N (2022) Sexual size dimorphism and male reproductive traits vary across populations of a tropical rainforest dung beetle species (*Onthophagus babirusa*). *Ecology and Evolution* 12: e9279. <https://doi.org/10.1002/ece3.9279>
- Torres-Vila LM (2017) Reproductive biology of the great capricorn beetle, *Cerambyx cerdo* (Coleoptera: Cerambycidae): a protected but occasionally harmful species. *Bulletin of Entomological Research* 107: 799–811. <https://doi.org/10.1017/S0007485317000323>
- Torres-Vila LM, Mendiola-Díaz FJ, Conejo-Rodríguez Y, Sánchez-González Á (2016) Reproductive traits and number of matings in males and females of *Cerambyx welensii* (Coleoptera: Cerambycidae) an emergent pest of oaks. *Bulletin of Entomological Research* 106: 292–303. <https://doi.org/10.1017/S0007485315000747>
- Torres-Vila LM, Mendiola-Díaz FJ, Sánchez-González Á (2018) Adult size and sex ratio variation of *Cerambyx welensii* (Coleoptera: Cerambycidae) in Mediterranean oak (Fagaceae) woodlands. *The Canadian Entomologist* 150: 334–346. <https://doi.org/10.4039/tce.2018.14>
- Torres-Vila LM, Mendiola-Díaz FJ, Sánchez-González Á (2017) Dispersal differences of a pest and a protected *Cerambyx* species (Coleoptera: Cerambycidae) in oak open woodlands: a mark-recapture comparative study. *Ecological Entomology* 42: 18–32. <https://doi.org/10.1111/een.12355>
- Tseng M, Kaur KM, Soleimani Pari S, Sarai K, Chan D, Yao CH, Porto P, Toor A, Toor HS, Fograscher K (2018) Decreases in beetle body size linked to climate change and warming temperatures. *Journal of Animal Ecology* 87: 647–659. <https://doi.org/10.1111/1365-2656.12789>
- Ulrich W (2007) Body weight distributions of central European Coleoptera. *European Journal of Entomology* 104: 769–776. <https://doi.org/10.14411/eje.2007.098>
- Venables WN, Ripley BD (2002) *Modern Applied Statistics with S*, 4th edn. Springer, New York. <https://doi.org/10.1007/978-0-387-21706-2>
- Vendl T, Kratochvíl L, Šípek P (2016) Ontogeny of sexual size dimorphism in the hornless rose chafer *Pachnoda marginata* (Coleoptera: Scarabaeidae: Cetoniinae). *Zoology* 119: 481–488. <https://doi.org/10.1016/j.zool.2016.07.002>
- Vendl T, Šípek P, Kouklík O, Kratochvíl L (2018) Hidden complexity in the ontogeny of sexual size dimorphism in male-larger beetles. *Scientific Reports* 8: 5871. <https://doi.org/10.1038/s41598-018-24047-1>
- Wang Q [Ed.] (2017) *Cerambycidae of the World*. CRC Press. <https://doi.org/10.1201/b21851>
- Warton DI, Duursma RA, Falster DS, Taskinen S (2012) smatr 3—an R package for estimation and inference about allometric lines. *Methods in Ecology and Evolution* 3: 257–259. <https://doi.org/10.1111/j.2041-210X.2011.00153.x>
- Warton DI, Wright IJ, Falster DS, Westoby M (2006) Bivariate line-fitting methods for allometry. *Biological Reviews* 81: 259–291. <https://doi.org/10.1017/S1464793106007007>

- Weber JN, Kojima W, Boisseau RP, Niimi T, Morita S, Shigenobu S, Gotoh H, Araya K, Lin C-P, Thomas-Bulle C, Allen CE, Tong W, Lavine LC, Swanson BO, Emlen DJ (2023) Evolution of horn length and lifting strength in the Japanese rhinoceros beetle *Trypoxylus dichotomus*. *Current Biology* 33: 4285–4297.e5. <https://doi.org/10.1016/j.cub.2023.08.066>
- Wickham H (2016) *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York. <https://doi.org/10.1007/978-0-387-98141-3>
- Zar JH (2010) *Biostatistical Analysis* (5th edn.). Upper Saddle River, NJ: Prentice-Hall/Pearson
- Zhu M, Niklas KJ, Chen L, Wang L, Jiao Y, Shi P (2025) Scaling relationships and sexual size dimorphism among the body parts of *Hototrichia oblita* (Coleoptera: Scarabaeidae). *Ecology and Evolution* 15: e71760. <https://doi.org/10.1002/ece3.71760>

Supplementary material 1

Locations of GPS coordinates of the sampling sites within Putna-Vrancea Natural Park, Eastern Carpathians, Romania

Authors: Marian D. Mirea, Iulia V. Miu, Lavinia C. Pindaru, Steluta Manolache, Laurentiu Rozylowicz
 Data type: docx
 Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
 Link: <https://doi.org/10.3897/bull.insectology.187568.suppl1>

Supplementary material 2

Image illustrating the picture acquisition methodology of saproxylic insects from the Eastern Carpathians, Romania

Authors: Marian D. Mirea, Iulia V. Miu, Lavinia C. Pindaru, Steluta Manolache, Laurentiu Rozylowicz
 Data type: docx
 Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
 Link: <https://doi.org/10.3897/bull.insectology.187568.suppl2>