Mammalian Biology
https://doi.org/10.1007/s42991-025-00508-9

ORIGINAL ARTICLE

Unmasking cryptic mice: the dominant role of ventral pelage colour in distinguishing syntopic *Apodemus (A. sylvaticus-A. flavicollis)*

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Received: 6 April 2025 / Accepted: 14 June 2025

Abstract

This study investigates the variability in morphometric (body size and pelage colour) traits to establish discriminant criteria for accurately identifying syntopic *Apodemus* species in NE Spain. Despite genetic divergence, in SW Europe these cryptic species present challenges in field identification due to their morphological similarities. Sampling campaigns were conducted in deciduous forests from Navarra and Barcelona, employing live-trapping methodologies, and individuals captured were accessioned as voucher specimens for biometric and colorimetric analyses. We found significant morphological and colorimetric differences between *A. flavicollis* and *A. sylvaticus*, namely large size and high pelage contrast in the former (higher lightness and chroma). Our results suggested that ventral colour variability was higher than dorsal, and ventral colour variables had stronger discriminating power among species. Indeed, a discriminant function, combining ventral colour and body size, allowed correct classification of 96.4% of the individuals among species. The dorsal coloration of both species was similar, suggesting convergent evolution driven by crypsis. Despite being the base of ecological studies on coat coloration (e.g., Gloger's rule), dorsal colour was less useful for differentiating species. Analysis of ventral coloration for species identification was normally dismissed by investigators, and we propose the need of potentially including ventral colour assessment when working with cryptic species. Our approach, using museum skins and a flatbed scanner with standardized illumination, yielded more precise coat colour data than internet images, allowing for detection of subtle chromatic variations. The integrated approach, combining biometric and colorimetric data, provided a robust framework for understanding the phenotypic variability and potential ecological adaptations of these closely related rodents.

Keywords Coloration · Museum flat skins · Discriminant analysis · Sympatric populations · Deciduous forests

Introduction

Pelage coloration in mammals is a complex trait, shaped by ecological pressures and summarized by ecogeographic rules (Cerezer et al. 2024). Gloger's rule, describing spatial variation in animal coloration (Delhey 2017), remains a particularly challenging principle, with camouflage often proposed as a primary driver (Delhey 2019). Historically, pelage coloration and body size were primary taxonomic markers in mammals (Mullen et al. 2009; Schiaffini 2020). However, genetic analyses have revealed the limitations of these purely phenotypic classifications, demonstrating that morphology does not always reflect genetic divergence (Mullen et al. 2009). Animal coloration serves diverse functions, including camouflage, communication, defence, and thermoregulation (Cuthill et al. 2017). Yet, relying solely on visual cues like size and colour poses significant challenges, particularly with cryptic species and sympatric sibling species (Bickford et al. 2007). While molecular data can resolve species boundaries, field identification often prioritizes easily observed features, reflecting a human bias towards visual processing. This bias is especially demanding in small mammals, where cryptic coloration is frequently favoured (Caro

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Handling editor: Germán Montoya Sanhueza.

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2005), and dorsal pelage colour frequently matches with the substrate to avoid predation (Hoekstra and Nachman 2005; Nokelainen et al. 2020). In syntopic (sharing the same habitat) small mammal species ecological convergence can lead to a striking similarity in coat colours, and even size. This phenomenon arises when species, despite having distinct evolutionary lineages, experience comparable selective pressures within their shared environment (Manceau et al. 2010). Under syntopic conditions, where external measurements are crucial for species differentiation, their reliability is significantly compromised (Kamler et al. 1998). To overcome the challenge of distinguishing syntopic cryptic species, a well-defined protocol for collecting tissue samples is crucial for subsequent molecular analysis and definitive species identification (Delciellos et al. 2018). This study proposes a low-cost, accessible, and non-invasive morpho-phenotypic alternative, applicable to museum collections: combining biometrics with standardized and detailed pelage colour analysis to improve species identification without necessarily relying on molecular techniques.

The wood mouse *Apodemus sylvaticus* (Linnaeus, 1758) and the yellow-necked mouse *Apodemus flavicollis* (Melchior, 1834), offer a compelling case study of such cryptic species. These two species occupy extensive and often overlapping (sympatric) distributional areas across many western and central European countries within the temperate zone of the Western Palearctic (Orlov et al. 1996). Their observed phenotypic similarity likely stems from a history of evolutionary divergence under convergent ecological selective pressures within European forest ecosystems (Michaux et al. 2002). Documented morphological overlap between these species, largely attributable to high intraspecific variability in body size and coat pigmentation of both species (Orlov et al. 1996; Kerr et al. 2017), makes it difficult to discern true species and population differences. Despite their overall similarity, subtle differences and ecological interactions exist between these species. It is often considered that character displacement and niche segregation are required for related, similar species to coexist, especially in shared habitats (Schluter 2000). To enable coexistence through specialized resource utilization, species are expected to exhibit differences not only in overall size (affecting food access) but also in biomechanical traits such as mandibular shape (Kerr et al. 2017). Notably, *Apodemus sylvaticus* and *Apodemus flavicollis* exhibit opposing north-south clinal variation in body size (Alcántara 1991), and *A. sylvaticus* shows a gradual increase in body size towards more southern latitudes, while the body size of *A. flavicollis* decreases. The presence of sexual size dimorphism in both species (Alcántara and Díaz 1996; Balčiauskas and Balčiauskienė 2025) contributes to an increase in size heterogeneity that even poses more difficulties to discriminate species based solely on morphological grounds. Consequently, due to interspecific morphological similarity compounded by high intraspecific variability, *A. flavicollis* and *A. sylvaticus* populations from Southern Europe display a reduced degree of morphological differentiation compared to those from Central and Northern Europe (Jojić et al. 2014; Bartolommei et al. 2016; Ancillotto et al. 2017), and some authors included molecular analysis in their sampling protocols (Bonacchi et al. 2021). Furthermore, other discriminant traits, such as the collar-like spot, largely present in central European *A. flavicollis*, becomes a small spot in southern populations, thus making separation more difficult. Recently, some discriminant criteria based on non-visual characters have been developed (distress calls, (Ancillotto et al. 2017), suggesting that solutions for the unambiguously determination of cryptic *Apodemus* can be achieved without using morphological traits.

In this study we investigated morphometric trait variability (body size and pelage colour) in syntopic *Apodemus* species inhabiting deciduous forests of NE Spain (Navarra and Barcelona). These species represent the majority of live captures in these forests (Torre et al. 2018) and are a primary food source for forest mesocarnivores (Torre et al. 2013). While dental morphology is valuable for identifying both species from prey remains (Torre et al. 2015), the examination of external morphological traits is critical for effective monitoring. This study aimed to define reliable visual criteria for accurate species differentiation. We predicted that subtle variations in size and colour would differentiate the analyzed species, with these differences reflecting the combined effects of geographic size clines variation in southern latitudes and ecological convergence in pelage colour for syntopic relatives.

Materials and methods

Apodemus sampling and species determination

Five sampling campaigns were carried out between May and June 1995 and May and September 1996 by one of the authors (A.A.), encompassing 18 different sites in northern Navarra (northeastern Spain). Furthermore, three surveys were performed during September 1996 at three localities within the Montseny Natural Park (Barcelona province, Fig. 1, Arrizabalaga et al. 1999). In this latter area, studies were conducted to establish the presence of the yellow-necked mouse, a species that was previously overlooked and considered absent from the Catalan territory (Gosálbez 1987). Standard live-trapping methodologies were employed, utilizing transects of 20–50 Sherman live traps (folding Sherman trap for small animals; 23 × 7.5 × 9 cm,

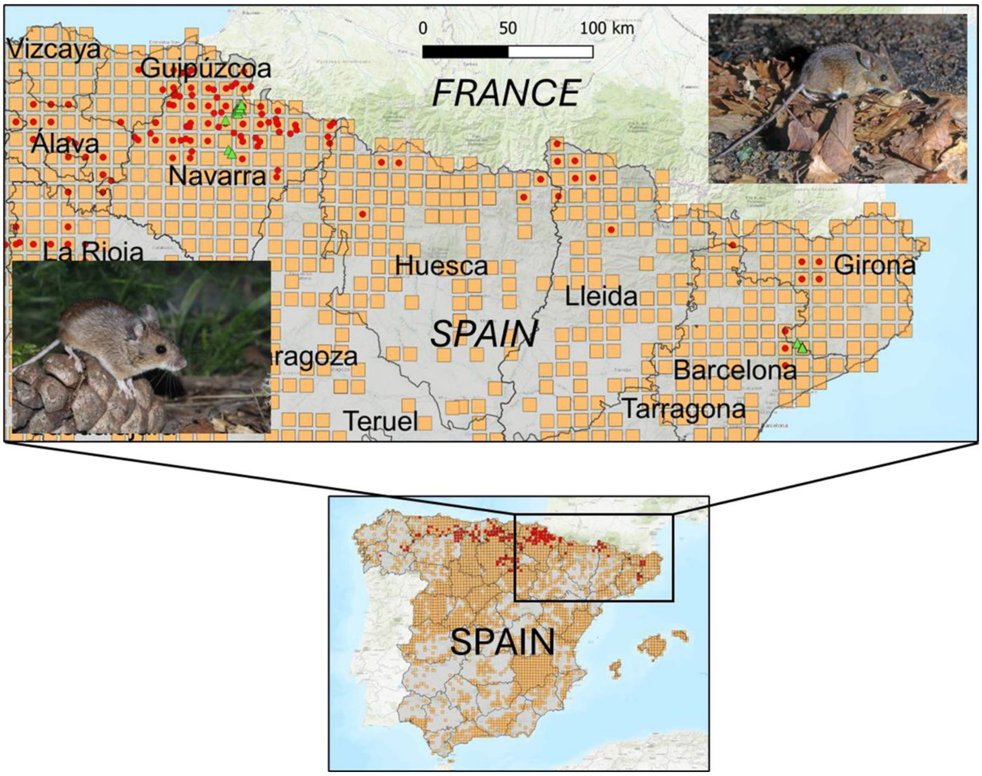


Fig. 1 Distribution of the localities (green triangles) where individuals of the genus *Apodemus* were sampled in the NE of the Iberian Peninsula (Navarra and Barcelona). The red dots show the known distribution of the yellow-necked mouse (*A. flavicollis*) and the orange squares the distribution of the wood mouse (*A. sylvaticus*) in 10 × 10 UTM grids of the Mammal Spanish Atlas (Palomo et al. 2007). Photos by I. Torre

Sherman Co., Tallahassee, FL, USA). Traps were deployed for a single overnight period, almost within deciduous forest habitats, specifically within beech (*Fagus sylvatica*) and sessile oak (*Quercus petraea*) forest communities. Only individuals of the genus *Apodemus* were euthanized in situ according to established protocols (Sikes and Animal Care and use Committee of the American Society of Mammalogists 2016), their skins and skeletal remains were prepared following standard procedures (Arrizabalaga and Uribe 1988), and individuals were accessioned as voucher specimens into the collection of the Granollers Museum of Natural Sciences. Mice captured in Barcelona were transported to the laboratory for protein electrophoresis analysis, following the protocol outlined by (Filippucci et al. 1989). The specific status of the individuals was identified with standard horizontal starch gel electrophoresis and scoring six diagnostic allozyme markers (Barčiová and Macholán 2009). Individuals were sexed and aged after necropsies (Balčiauskas and Balčiauskienė 2025), and only adults were considered in further analyses. The relative age of individuals was assigned considering the coats and moults, altogether with the reproductive condition (Sans-Coma et al. 1987).

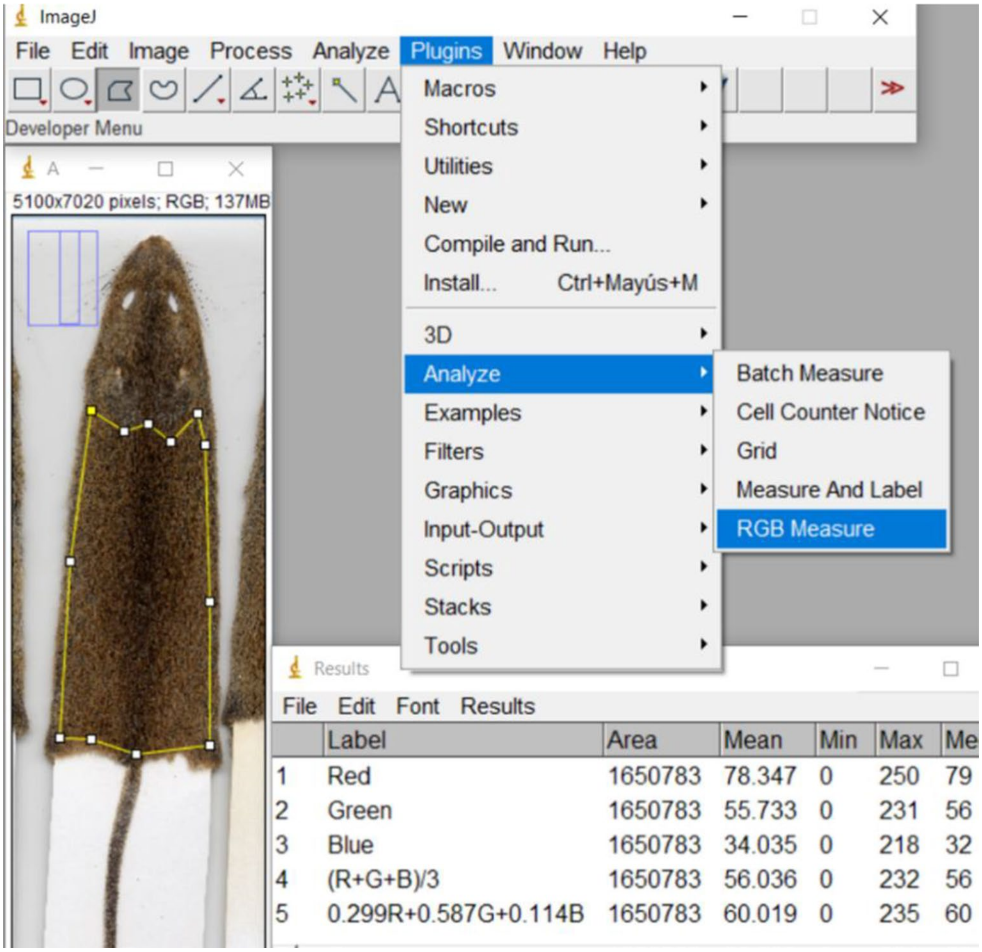
On a second step, we analysed the congruence between the molecular results and the dental morphological criteria. The complete coincidence observed allowed us to confidently use the dental criteria for species identification of the individuals from Navarra. Upper mandibles were positioned on a plasticine support and examined microscopically. Species identification was based on morphological distinctions in the shape of the molar tubercles (*t*) between the two syntopic species. This criterium followed a well-established methodology (Filippucci et al. 1989; Libois et al. 1993; Panzironi et al. 1993; Marchand and Denys 2003). Specifically, the identification criteria included: (1) the presence of a *t9* on the second upper molar in *A. sylvaticus*, which is absent in *A. flavicollis*. In case of failure of the former criterium due to molar erosion, we used (2) the presence of a distinct *t7*, clearly separated from *t4*, on the first molar in *A. flavicollis*, versus the fusion of these tubercles in *A. sylvaticus* (Torre et al. 2015).

Morphometry and coloration

Biometric measurements were taken using standard procedures (Gosálbez 1987; Arrizabalaga and Uribe 1988), with all linear dimensions recorded in millimetres. Weight was measured in grams using a dynamometer (Pesola AG, Baar, Switzerland; precision: 0.5 g). The following measurements were obtained with a Vernier caliper or a ruler (precision 1 mm): Tail Length (TL): Distance from the angle formed by the proximal ventral base of the tail and the posterior margin of the anal prominence to the distal tip of the tail, excluding terminal hairs. Head and Body Length (HBL): Distance from the tip of the snout to the proximal vertex defined in the TL measurement. Ear Length (EL): Maximum distance from the lower notch to the distal margin of the ear. Hind Foot Length (FL): Distance from the distal end of the longest digit (excluding the nail) to the posterior margin of the heel. Animals were weighed and measured prior to necropsy (Balčiauskas and Balčiauskienė 2025).

Quantification of pelage coloration presents challenges due to its dependence on incident light. Digital photography, while a common method (Davis et al. 2013; Boratyński et al. 2014; Stanchak and Santana 2019; Cerezer et al. 2024), for our case was deemed unsuitable due to the inherent difficulties in standardizing illumination parameters. Therefore, flat skin samples were scanned using an *EPSON perfection 2450 photo* scanner to achieve greater control over illumination variables (Fig. 2). Prior to scanning, the scanner was calibrated using ICC profiles to ensure colorimetric accuracy. The ICC profile was specifically designed to transform the scanner's native colour space to the sRGB colour space. Importantly, all samples were processed during the same period (spring 2013) and under identical machine settings, allowing for direct comparisons of pelage coloration across specimens within the study period. Given that all individuals were captured within a narrow temporal window (1995–1996), we anticipated some degree of pigment degradation between the time of sampling and the time of colour analysis (Sandoval Salinas et al. 2018; Jou et al. 2025), spanning approximately two decades (1995–2013). Consequently, while the measured pelage colour may not precisely reflect the current pelage characteristics of extant populations (Davis et al. 2013), we expect that the colorimetric analyses were not systematically biased across the years under comparison. Nonetheless, we did not perform a comprehensive scanner characterization, including assessments of spectral linearity, spatial homogeneity, noise levels, and repeatability. A comprehensive protocol previous to colorimetric analysis is necessary to reach high standards of scanner accuracy and reliability, similar to those reported for digital photography (Troscianko and Stevens 2015).

Following scanning, ImageJ software (https://imagej.net/ij/; Abràmoff et al. 2004) was employed for colorimetric analysis. Red, green, and blue (RGB) values were extracted, and the average RGB value (R + G + B/3) was used to quantify pelage brightness or intensity (Boratyński et al. 2014; Stanchak and Santana 2019; Cerezer et al. 2024). The average RGB value was used as a proxy for eumelanin pigment concentration, while the ratio of red to the average RGB value served as a proxy for pheomelanin concentration,



	Label	Area	Mean	Min	Max	Me
1	Red	1650783	78.347	0	250	79
2	Green	1650783	55.733	0	231	56
3	Blue	1650783	34.035	0	218	32
4	(R+G+B)/3	1650783	56.036	0	232	56
5	0.299R+0.587G+0.114B	1650783	60.019	0	235	60

Fig. 2 Flat skin colour processing: Flat skin of *Apodemus flavicollis*, with the area selected (yellow) and RGB analysis using ImageJ software (https://imagej.net/ij/) showing the area sampled (in pixels) and the descriptive statistics of the RGB colours

thereby quantifying pelage redness (Cerezer et al. 2024). To ensure accurate colour measurement, dorsal and ventral image regions were carefully selected and framed (Boratyński et al. 2014), maximizing the analyzed area while excluding damaged portions of the skin (Fig. 2). This method of colorimetric analysis was more objective, and we believe that outperforming visual methods such as using a pelage melanisation chart (Howell and Caro 2024). Furthermore, for each individual within each species, we calculated standard colour metrics in the CIELAB colour space and the distance between the mean colour values of the dorsal and ventral regions was computed using a reduced version of the formulae (Sharma et al. 2005). This difference was quantified using the Euclidean distance in lightness and colour in the CIELAB color space (ΔE), a standard metric for perceived colour dissimilarity that is more aligned with human visual perception than would be possible using a device-dependent colour space like RGB:

$$\Delta E = \sqrt{\left(L_D^* - L_V^*\right)^2 + \left(a_D^* - a_V^*\right)^2 + \left(b_D^* - b_V^*\right)^2}$$

Lightness (L*): Ranges from 0 (black) to 100 (white) and represents an achromatic channel.

a* (Green-Red): Ranges from negative values (perceived as greener) to positive values (perceived as redder).

b* (Blue-Yellow): Ranges from negative values (perceived as bluer) to positive values (perceived as yellower).

Despite both conventional, more used RGB profiles, and alternative (CIELAB) colour spaces performed similarly for quantifying pelage colour (Cerezer et al. 2024), the latter is generally recommended for biological studies due to its basis in the human visual model, encompassing the full spectrum of human-perceived colours (Sandoval Salinas et al. 2018). Finally, another characteristic we wanted to focus on was the pectoral spot that individuals of these species exhibit. As we mentioned earlier, in some areas of northern and central Europe, differences in this trait are observed, with the spot present in *A. flavicollis* specimens being larger, sometimes to the point of forming a collar. For these reasons, we measured the length and width of this spot. Because the skin mounting process can cause stretching when the cardboard is inserted, we eliminated this effect by measuring the chest width of the individual, the width of the spot, and looking at what percentage of the chest this occupied. As we understand that stretching affects the entire skin in the same way, the fact of using a percentage eliminates the effect and error that the stretching would produce.

Data analyses

We employed the comprehensive statistical protocol of (Zuur and Ieno 2016) to ensure robust analyses. Prior to analyses, all variables were scaled to zero mean and unit standard deviation. The initial exploration of variable distributions revealed that colour variables followed a Gaussian distribution (Shapiro-Wilk tests, all $p > 0.05$). Conversely, many biometric variables failed to achieve normality. In a second step, two principal component analysis (PCA) were performed to reduce dimensions and to analyse patterns of covariation in the two sets of biometric (weight, HBL, TL, FL, EL) and colour pelage (RGB/3, Red, Green and Blue for either dorsal and ventral sides, pectoral spot size) variables. These new variables can be interpreted as gradients with biological and ecological meaning and were used as response in further analyses (Dytham 2011). Regarding morphometric data, the first extracted component summarizes isometric size alone, and the second component contrasts allometric patterns of covariation among characters, representing variation in relative shape (Somers 1986).

To investigate morphometric and colorimetric differences between *A. flavicollis* and *A. sylvaticus* (species), between sexes (female and male), and the interaction between species and sex, we used generalized linear mixed-effects models with a Gaussian distribution to model the response variable and identity as link function (GLMMs, Bolker et al. 2009). Two principal components, extracted from size and colour (RGB) datasets respectively, served as response variables. Species, sex, and their interaction were included as fixed effects. Spatial dependence among observations was accounted for by incorporating locality as a random intercept. Since all individuals were obtained in spring-summer, we did not take account of seasonal variation in coat coloration. This source of variability (if present) will be captured by the random effect of the statistical models. Multicollinearity between predictors was assessed using variance inflation factors (VIFs), and fixed factors were centred by creating sum-to-zero contrasts (dummy variables). Model fit was evaluated via residual analysis using the *DHARMa* package (Hartig 2022), assessing their uniformity and dispersion. Model performance was determined by comparing the corrected Akaike Information Criterion (AICc) of the full model to that of a null model containing only the intercept and random effect. We also calculated pseudo-R^2 values by means of the R function *r.squaredGLMM* and the delta method for variance estimation (Nakagawa and Schielzeth 2013). To fit the models we used the *lmer* function in the *lme4* R package (Bates et al. 2015). Full statistical contrasts *Species: Sex* were analysed by estimated marginal means using the *emmeans* package (Lenth 2023), applying the Bonferroni correction for multiple pairwise comparisons.

For PCA plots we used the *factoextra* package (Kassambara and Mundt 2020), and for the correlation matrices the package *corrplot* (Wei and Sim 2017). Conversion of sRGB to CIELAB colour space was performed with the *colorspace* package. Finally, we analysed the simultaneous effects of biometry and pelage colour on the species by means of linear discriminant analysis (LDA). All analyses and figures were performed under the R and RStudio environments (R Core Team 2023; R Studio Team 2020), and species maps were performed with QGIS (v 3.22, https://qgis.org).

Results

The sampling campaigns conducted in Navarra yielded 129 *Apodemus* (32 in 1995 and 97 in 1996), and the sampling campaign conducted in Barcelona in 1996 yielded 6 *A. flavicollis* and 23 *A. sylvaticus* (molecular analysis). After applying the molar criteria to the unidentified individuals from the Navarra samples, 23 were assigned to *A. flavicollis* and 103 to *A. sylvaticus*. Therefore, *A. flavicollis* represented the 18.2% and 20.7% in Navarra and Barcelona, respectively. Congeneric individuals shared 10 out of 18 sites (55.5%) in Navarra, and two out of three sites in Barcelona. *Apodemus sylvaticus* was captured in 13 localities at a mean elevation of 783 m.a.s.l. (560—1,120), and *A. flavicollis* was captured in 8 localities at a mean elevation of 870 m.a.s.l. (660—1,120). After gonadal examination, 106 individuals were considered adults in Navarra (82.1%), but only 12 were adults in Barcelona (41.4%). The final dataset, with complete biometric information contained 88 individuals (66 *A. sylvaticus* and 22 *A. flavicollis*), and the dataset with complete colorimetric data contained 89 individuals (66 *A. sylvaticus* and 23 *A. flavicollis*). After gathering both biometric and colorimetric information within a single dataset we obtained a sample of 84 individuals (64 *A. sylvaticus* and 20 *A. flavicollis*). Inconsistencies between the biometric and colorimetric datasets were caused by the absence of flat skins (or having damaged areas, e.g., ears) for some biometric data, and vice versa. However, GLMMs take account of the whole samples available since biometric and colorimetric responses were analysed separately, and only the discriminant analysis, which simultaneously analysed the influence of both biometric and colorimetric predictors, was performed on the reduced sample size.

We conducted two principal component analyses (PCAs) – one using five body size measurements from 88 individuals and another using nine pelage colour variables from 89 individuals. The body size PCA yielded two components: PC1(size), representing overall body size (positive loadings for all variables, explaining 46.7% of the variance), and PC2(size), capturing allometric relationships (negative loadings for weight and head-body length, positive loadings for the three appendage measurements (20.1% of the variance; see Fig. A in Suppl. Materials). The pelage colour PCA also extracted two components: PC1(rgb), summarizing ventral coloration and spot size (negative loadings for all variables, explaining 46.1% of the variance), and PC2(rgb), representing dorsal coloration (positive loadings, explaining 40.1% of the variance, see Fig. B in Suppl. Materials). The five significant components resulting from the CIELAB PCA did not include one that clearly separated dorsal and ventral colours, thus making its application to species discrimination significantly more complex (see Fig. C in Suppl. Materials).

Colour and size variability among species

For both species, the pelage exhibited a clearly bicolour pattern in dorsal view (Fig. 2), featuring a brown dark dorsal stripe extending along the entire body from the head to the tail base, and two flanks with a lighter brown coloration that merged with the uniform white/grey of the ventral region. Significant interspecific differences were observed across most pelage colour variables, particularly on the ventral side (Fig. 3). In the CIELAB space, one out of five variables showed interspecific differences in dorsal side, but four out of five variables showed differences in ventral side (Fig. 3). Once a Bonferroni correction was applied to account for multiple tests of related variables (resulting in a new significance threshold of $p = 0.01$), the previously significant dorsal difference in the identified variable was no longer statistically significant (all ventral variables remained significant). Nonetheless, dorsal differences were still evident in three out of four metrics on the RGB space (see Fig. D in Suppl. Materials) after a Bonferroni correction. *Apodemus flavicollis* displayed a ventral pelage that was characterized by higher lightness (L*) and chroma (C*), as well as a shift towards yellower (b*) and greener (a*) regions of the colour spectrum. *Apodemus flavicollis* pelage also presented more contrasting patterns, attributable to pronounced differences between dorsal and ventral coloration (Fig. 4a). Countershading, the contrast between dorsal and ventral pelage coloration (ΔE), was higher in *A. flavicollis*, but both syntopic species showed a similar pattern of change along the sampled localities (Fig. 4b). GLMMs using PC1 (rgb), which summarized ventral pelage brightness and pectoral spot size, revealed significant differences between species (Table 1). *Apodemus flavicollis* exhibited higher brightness and larger pectoral spots on the ventral side compared to *A. sylvaticus*. No significant sexual dimorphism in ventral coloration or species-by-sex interaction was observed (Table 1). This model demonstrated good fit (uniform and undispersed residuals) and outperformed the null model,

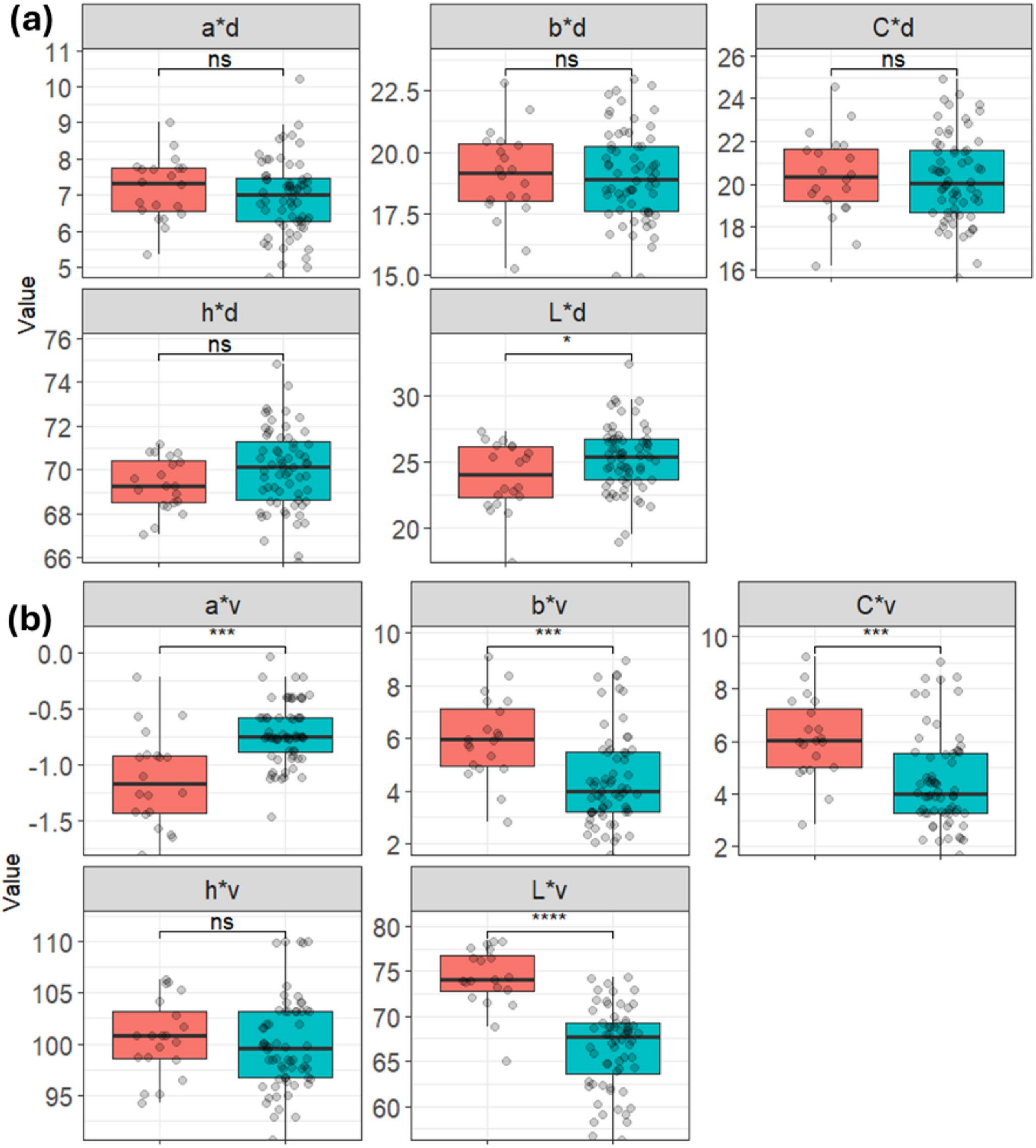


Fig. 3 Boxplots (median ± interquartilic range) for the five metrics in the CIELAB colour space for the dorsal **(a)** and ventral **(b)** pelage in *A. flavicollis* (coral red) and *A. sylvaticus* (teal), and statistical comparisons between the species tested by t-tests. P-values: *: $p<0.05$; **: $p<0.01$; ***: $p<0.001$; ****; $p<0.0001$; ns = non-significant

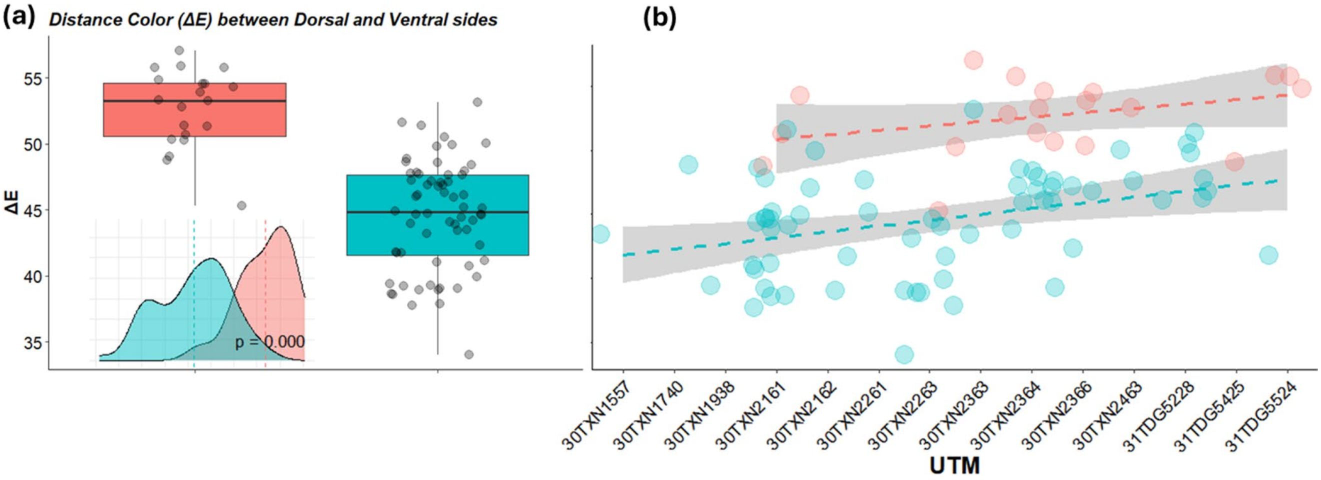


Fig. 4 **(a)** Differences (boxplot and density plot) in the contrast of pelage coloration of *A. flavicollis* (coral red) and *A. sylvaticus* (teal) quantified as the Euclidean distance between the mean colour values of the dorsal and ventral regions in the Lab colour space (ΔE). **(b)** Similarity of pelage contrast between syntopic species along the sampled localities (UTM units from West to East). Shaded areas along the regression lines are CI ± 95%

Table 1 Results of the four GLMMs (with a Gaussian distribution to model the response variable and identity as link function) with the four principal components summarising colour (RGB) and size variation in *Apodemus*, and the fixed effects species, sex, and their interaction, and the locality as a random effect. The table shows the estimated coefficients (±SE), the p-value, the variance explained by the fixed (marginal R^2) and the whole model (fixed + random effects, conditional R^2), the model fit (AICc) compared to the null model (intercept only), and the distribution of residuals. Significant results in bold ($p < 0.001$), and marginal in italics ($p < 0.1$)

Term	PC1 (rgb) ventral colour		PC2 (rgb) dorsal colour		PC1 (size) isometric		PC2 (size) allometric	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
(Intercept)	–0.67	0.34	–0.06	0.37	0.30	0.28	0.28	0.20
Species (*A. flavicollis*)	**–1.43**	0.24	–0.45	0.37	**0.97**	0.26	0.24	0.20
Sex (male)	0.31	0.23	0.24	0.37	–0.13	0.26	0.37	0.20
Species: Sex	–0.12	0.23	–0.04	0.37	*0.45*	0.26	0.28	0.20
Marginal R^2	0.46		0.06		0.26		0.04	
Conditional R^2	0.64		0.06		0.31		0.05	
AICc	288.24		357.34		297.66		249.61	
AICc null	341.95		355.59		316.35		246.42	
Delta AICc	–53.71		1.76		–18.69		3.19	
Uniformity (p)	0.73		0.82		0.21		0.14	
Dispersion (p)	0.61		0.93		0.87		0.93	

with fixed effects explaining 46% of the variance (i.e., 72% of variance of the model explained by the fixed effects). In contrast, PC2 (rgb), which captured dorsal colour variation, did not show significant differences between species or sexes, suggesting limited variation in dorsal coloration. However, for both species there were no significant correlations between colour variables for dorsal and ventral views, suggesting that coloration in both body sides was, somehow, independent.

A distinct white margin on the ears, formed by short white hairs primarily along the edge, was a common trait in *A. sylvaticus* (78%) but rare in *A. flavicollis* (<5%, Fig. 5). However, detailed macrophotographic analysis revealed that this margin could be present, albeit less conspicuous, in individuals initially classified as lacking it (see Fig. F in Suppl. Materials).

The size of the chest spot differed between species, measuring 32.1% ± 3.0 SE in *A. flavicollis* and 12.1% ± 1.2 SE in *A. sylvaticus* (Fig. 6). In both species, a difference was also observed between sexes: the spot was large in females (*Af*: 43.2% ± 4.6 SE; *As*: 16.4% ± 1.8 SE) compared to males (*Af*: 29.8% ± 2.1 SE *As*: 10.7% ± 1.4 SE), but differences were non-significant (Fig. 6). However, none of the individuals showed a complete spot-like-collar.

Apodemus flavicollis showed higher mean weight, head and body length, and tail length than *A. sylvaticus*, and hence for PC1(size, see Fig. E in Suppl. Materials). A GLMM using PC1(size), representing overall body size, revealed significant differences between species (Table 1). No significant

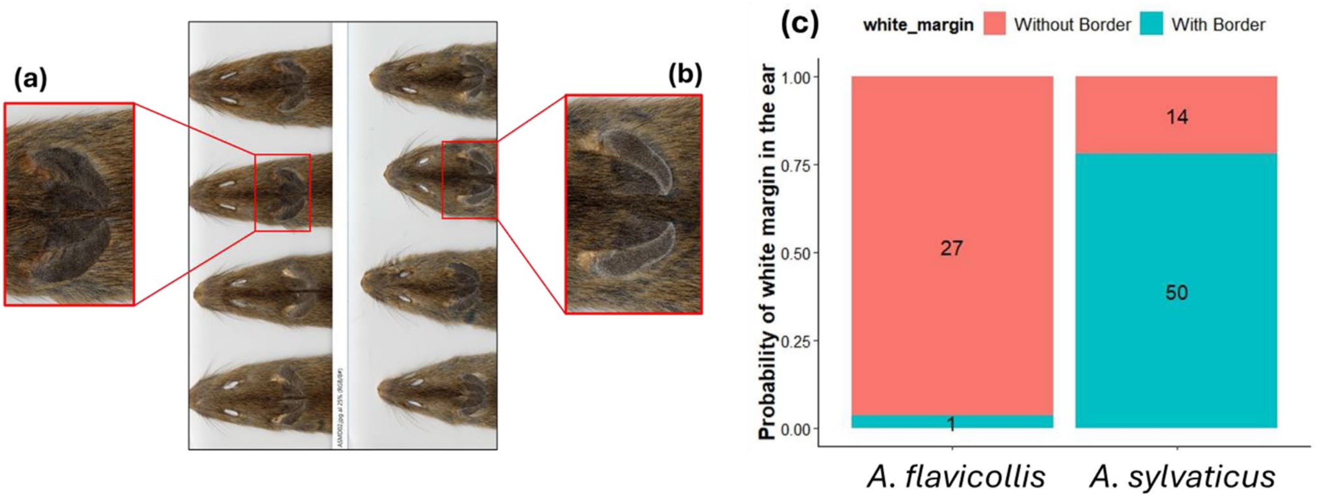
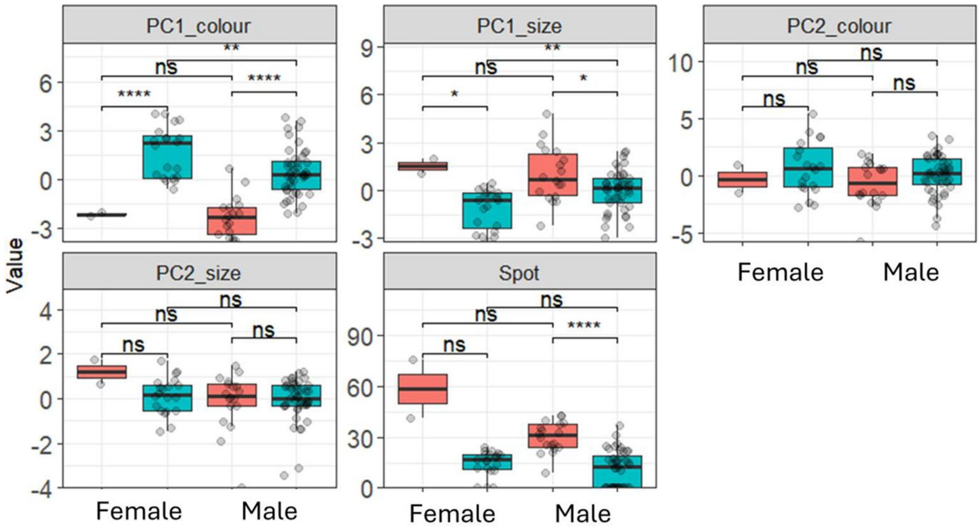


Fig. 5 Presence/absence of the white margin along the external border of the ears in *A. flavicollis* **(a)** and *A. sylvaticus* **(b)**, and contingency table summarising the presence or absence of the attribute in the flat skins **(c)**

Fig. 6 Boxplots (median ± interquartilic range) of the four principal components summarising colour (PC1 = ventral; PC2 = dorsal) and body size (PC1 = isometric; PC2 = allometric), and size of the pectoral spot, by species and sex in *A. flavicollis* (coral red) and *A. sylvaticus* (teal). P-values for multiple comparisons, calculated with estimated marginal means, are significant at p-level = 0.05/4 = 0.0125, after a Bonferroni correction. P-values: *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$; ****; $p < 0.0001$; ns = non-significant



sexual dimorphism in body size was observed, despite a marginal species-by-sex interaction (Table 1). This model demonstrated good fit (uniform and undispersed residuals) and outperformed the null model, with fixed effects explaining 26% of the variance (i.e., 84% of variance of the model explained by the fixed effects). Estimated marginal means for each of the four contrasts *Species: Sex* highlighted that males and females *A. flavicollis* showed similar body size, but males *A. sylvaticus* were larger than females ($p < 0.01$, Fig. 6). In contrast, PC2(size), representing allometric relationships, did not show significant differences between species, but revealed a marginal difference between sexes, suggesting slight variations in relative appendage size. Estimated marginal means for each of the four contrasts *Species: Sex* highlighted that males and females *A. flavicollis* showed similar pelage colour in dorsal and ventral views, but males *A. sylvaticus* showed more colour intensity than females in ventral view (Fig. 6).

A Linear discriminant analysis (LDA) utilizing the four principal components, which encapsulated size and colour variability of the two *Apodemus* species, achieved a classification accuracy of 96.4%. Specifically, 18 out of 20 *A. flavicollis* and 63 out of 64 *A. sylvaticus* specimens were correctly classified (Fig. 7). PC1 derived from colour data exhibited the highest discriminatory power, followed by PC1 derived from size data and PC2 derived from colour data. PC2 derived from size data demonstrated negligible discriminatory power.

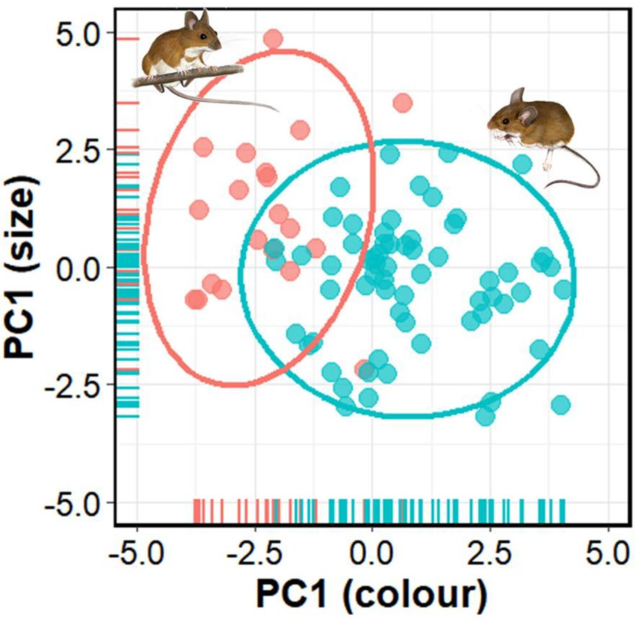


Fig. 7 The distribution of individuals of *A. flavicollis* (coral red) and *A. sylvaticus* (teal) in the discriminant bidimensional space generated by the PC1(colour) and PC1(size). The discriminant function including the four PCs allowed almost a perfect separation of the individuals by species (96.4%)

Discussion

This study investigated morphological and colorimetric differences between *Apodemus flavicollis* and *Apodemus sylvaticus* in NE Spain (Navarra and Barcelona). This is a comprehensive analysis of external morphology in sympatric and congeneric *Apodemus* species living in syntopy (i.e., sharing the same habitats). Our findings aligned with previous reports of larger body dimensions and greater pelage contrast in *A. flavicollis* (consistent with observations elsewhere in Europe: Alcántara 1991; Barčiová and Macholán 2009; Jojić et al. 2014; Bartolommei et al. 2016; Ancillotto et al. 2017). Additionally, our results suggested an ecological convergence of dorsal pelage colour between the two species, likely driven by crypsis (Mullen and Hoekstra 2008; Manceau et al. 2010). This convergence could be supported by the similarity of interspecific dorsal coloration, both species showing strong dorsal-ventral colour contrast, and a longitudinal dark dorsal stripe. But the most notable findings of this study revealed a strong species-discriminating power associated with ventral coloration, surpassing that of biometric traits.

The evolutionary divergence of *A. sylvaticus* and *A. flavicollis* into separate species, a process likely driven by allopatric speciation from a common ancestor (Michaux et al. 2002), was strongly influenced by differing environmental conditions in geographically isolated regions (SW and Central Europe). After expanding their ranges, they came into contact and subsequently developed some divergence in sympatric populations. Indeed, morphometric interspecific differences were noted throughout the distribution of *A. sylvaticus* and *A. flavicollis*, but these became less pronounced in southern Europe, where the two species tended to converge in size (Alcántara 1991). This size convergence in the south was mainly driven by ecogeographical rules and character displacement. The Bergmann-positive size gradient of the dominant *A. flavicollis* (larger at higher latitudes) likely constrained *A. sylvaticus* from exhibiting an opposite geographic size trend. Even the size convergence at southern latitude, the differentiation of both species is still possible based on morphometric measurements, like weight and foot length (e.g., Italy: Bartolommei et al. 2016; Ancillotto et al. 2017). These authors documented an interspecific weight difference of about 3–4 g, which was sufficient for discriminating. In our studied populations, however, differences were slightly lower (2.3 g: 22.56 g ± 0.33 vs. 24.76 g ± 0.87), but still significant in combination with other morphometric dimensions (body and tail length). Despite a lack of significant sexual size dimorphism (SSD) in our *A. flavicollis* population (likely due to sample size), we noted colour differences, with females having a larger neck spot. This contrasts with the generally male-biased SSD in European yellow-necked mice, though some populations are monomorphic (reviewed by Balčiauskas and Balčiauskienė 2025). The evidence suggests that this species exhibits short-term plasticity in body size, a characteristic that likely contributes to its ability to adapt to environmental modifications (Balčiauskas and Balčiauskienė 2024). *A. sylvaticus* is considered a sexually dimorphic species throughout its distribution range, males being larger than females (Sarà and Casamento 1995; Alcántara and Díaz 1996; Chassovnikarova and Markov 2007), and our population also was dimorphic.

Some investigations have focused solely on dorsal colour assessments to study pelage variability along strong geographic gradients (Cerezer et al. 2020, 2024), reflecting the general body coloration of rodent species (Caro 2013). While this approach is justifiable when examining the role of crypsis under specific ecogeographical rules (e.g., Gloger's rule), ventral coloration was disregarded in this context due to pre-existing assumptions of limited interspecific variation (Caro 2013; Cerezer et al. 2024). Our results suggested that ventral colour variability was higher than dorsal, and ventral colour variables had stronger discriminating power among species. Indeed, a discriminant function combining ventral colour and body size allowed correct classification of 96.4% of the individuals, a higher ratio of accuracy than observed for other sympatric populations in SW Europe (Bartolommei et al. 2016). A recent study on bank voles' morphometry using the same approach

(Jou et al. 2025) gave further evidence to our conclusions. These authors showed that ventral colour was more variable along the environmental gradient studied than dorsal colour. Since both dorsal and ventral coloration are controlled by the same antagonistic genes in rodents (Vrieling et al. 1994; Hoekstra and Nachman 2005; Manceau et al. 2010), colour differences between back and belly could represent the different influence of the environment in the dorsal and ventral sides. The weak differentiation in dorsal pelage colour between the sympatric *Apodemus* species points to crypsis as a possible factor promoting convergent dorsal coloration, as found in New World ecological equivalents (Hoekstra and Nachman 2005; Manceau et al. 2010). In contrast, this suggests that environmental pressures might play a different role in shaping ventral coloration. This could be supported by the lack of association between dorsal and ventral colour metrics analysed, suggesting that pelage colour on both sides evolved rather independently. Investigations on *M. musculus* indicates that ventral colour matches with geographic races, suggesting a genetic component (Takeishi et al. 2021). Nevertheless, alternative studies propose that ventral coloration changes in relation to dorsal coloration to create pelage contrast, consistent with a countershading mechanism (Caro 2009).

For the two mouse species inhabiting the same habitats, the dorsal pelage presented a notably similar bicoloured arrangement. This consisted of a dark brown stripe running along the entire dorsal surface from the head to the base of the tail, with lighter brown flanks transitioning into the white or grey ventral region. The strong dorsal-ventral colour contrast, especially in *A. flavicollis*, suggests countershading (i.e., self-shadow concealment), a cryptic mechanism that reduces the perception of three-dimensional forms in terrestrial environments (Caro 2009, 2013). However, this contrasting pattern is a common coloration phenotype in animals, with some instances arising from non-camouflage functions such as thermoregulation and UV protection (Allen et al. 2012). Furthermore, the dark brown dorsal stripe could act as disruptive colouration, generating false edges and boundaries that visually break up the animal's outline (Cuthill et al. 2005; Stevens and Merilaita 2009). Effective concealment is achieved when an individual's overall body colour aligns with its background environment (Singaravelan et al. 2010), a concept central to the prevailing interpretation of Gloger's rule (Delhey 2019). In small mammal prey, pelage colour plays a significant role in predator avoidance, with natural selection favouring cryptic patterns – hair colours that mimic the environment – as an anti-predator adaptation (Hoekstra and Nachman 2005; Caro and Mallarino 2020; Nokelainen et al. 2020). Sympatric wood mice (*Apodemus* spp.) were the most abundant small mammals in the study area. They constituted 60% of captures in natural habitats (forests and scrubland, Torre et al. 2018) and over 80% of the prey for some forest mesocarnivores (*Genetta genetta*, Torre et al. 2013), highlighting significant predation pressure on these rodents. Even forest diurnal raptors, such as the common buzzard (*Buteo buteo*), also preyed on wood mice according to their availability in the study area, with this being a key factor in increasing raptor productivity and affecting breeding phenology (Torre et al. 2024). Therefore, crypsis could be hypothesised as a primary selective pressure influencing dorsal coat coloration in these nocturnal small mammals driving to background matching (Nokelainen et al. 2020), which results in the predominantly dull brown and grey coloration observed across most species (Caro 2005, 2013). Analyses of dorsal pelage colour for both species demonstrated differences in both RGB and CIELAB colour spaces. In the first colour space there were more interspecific differences, and both species showed a dominant red component, followed by green, and a significantly reduced blue component. The reddish dorsal pattern (indicative of higher pheomelanin content) was typical for rodents living in areas with high precipitation and temperature (Cerezer et al. 2024). The rainy and temperate climate (precipitation > 1,000 mm, temperature = 9.5 ºC) altogether with the sampled habitats (mostly *Fagus sylvatica* deciduous forests) were similar enough in the two study areas to allow for combined analysis. Further support on the role of crypsis on coat coloration is provided by a recent study on bank voles (*Clethrionomys glareolus*) in the same area, where individuals from deciduous forests displayed redder dorsal colour compared to those from sclerophyllous forests (Jou et al. 2025). These findings would suggest that crypsis will be modelling the dorsal pelage of small rodents of different lineages living in similar habitats to mimic the environment. Alternatively, the high red component of colour in dorsal and ventral views in both species could well be a consequence of eumelanin pigment degradation with time, making red colours to emerge in old museum skins (Davis et al. 2013). Some authors pointed out that colour patterns showed differential melanin degradation between dorsal and ventral sides of the flat skins (Jou et al. 2025), raising concerns about the accuracy of museum specimens in representing the true coloration of living animals (Sandoval-Salinas et al. 2018). Consequently, to evaluate its effects, it is necessary to analyse the colour of extant populations against the old samples collected several decades ago.

Recent studies on pelage colouration relied on digital images on the Internet as the primary resource for rodent comparative studies (Cerezer et al. 2024). This allowed the obtention of hundreds of images of several species, contributing to generate large multi-specific datasets associated to environmental gradients for making strong inferences for macroecological studies. Nevertheless, it is important to acknowledge that digital images obtained from heterogenous sources can introduce many biases, such as taxonomic errors (e.g., incorrectly determining cryptic species) or overlooked ontogenetic and seasonal changes in pelage coloration. But even more important, the use of images from digital cameras needs to be submitted to a comprehensive evaluation and standardization of each image previous its inclusion in the dataset (Stevens et al. 2007; Troscianko and Stevens 2015), rising doubts about the reliability of chromatic information. Similarly, even without verifying constant and uniform scanner light, data accuracy and reliability require addressing the sensor's linearity, spatial homogeneity, and noise levels, highlighting the necessity of a comprehensive characterization protocol analogous to those in digital photography. Despite the application of sophisticated techniques like spectroradiometry in small mammal coat colour research, a significant gap remains: the consistent focus on dorsal (or lateral) perspectives of the body (Sandoval Salinas et al. 2017, 2018; Cerezer et al. 2024; Howell and Caro 2024). Ventral coloration was largely ignored as a potential driver of intra- and interspecific variation (see however, Manceau et al. 2011; Takeishi et al. 2021), an oversight often justified by pre-conceived notions of ventral colour's irrelevance in some groups of rodents, at least at the intra-specific level (Carraway and Verts 2002; Cerezer et al. 2024). To address this, we advocate for utilizing museum study flat skins and the simultaneous analysis of both dorsal and ventral surfaces under standardized light (via flat scanner). This will allow us to identify spatial covariation in pelage and differentiate between environmentally driven (dorsal-lateral) colour patterns and those likely reflecting a stronger genetic influence. The foundational research of Gloger (1883, quoted by Rensch 1938), which documented geographical coat colour patterns through the examination of museum specimens, exemplifies this approach.

Conclusions

This study demonstrates significant morphological and colorimetric differences between *A. flavicollis* and *A. sylvaticus*, which can be effectively used to differentiate these species. The dorsal coloration of both species was similar, suggesting convergent evolution driven by crypsis (blending in with the environment to avoid predators). This convergence makes dorsal coloration less useful for differentiating species. In contrast, the greater divergence in ventral coloration suggests being less subject to environmental selective pressures and making it a better indicator of species identity. Analysis of ventral colouration for species identification was normally dismissed by investigators, and we propose the need of potentially including ventral colour assessment when working with these species. This unexpected result emphasizes the importance of considering these pronounced species-specific differences when establishing discriminatory criteria based on external morphological characteristics. The utilization of museum study skins and flatbed scanners under standardized illumination allowed obtaining more precise and comparable data which facilitates the detection of subtle chromatic variations that may be overlooked by conventional techniques. But a notable constraint of our methodology is its inherent dependence on planarized museum specimens and controlled laboratory conditions for scanning. This limitation precludes its application to in situ analyses of live subjects or the assessment of volumetrically preserved material, and our technique necessitates a specific preparation protocol for compatibility with flatbed digitization.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s42991-025-00508-9.

Acknowledgements This article was inspired by a Degree Thesis presented by Alba Capdevila at the Faculty of Biological Sciences of the University of Barcelona (UB) in September 2013 and directed by Ignasi Torre. The pictures of mice were kindly provided by Alfons Raspall. The comments of two anonymous reviewers, the Associate Editor, and the Editor in Chief improved the final version of this article.

Author contributions Conceptualization: IT; Methodology: AC, AA, IT; Formal analysis and investigation: AC, IT; Writing - original draft preparation: IT; Writing - review and editing: IT; Data curation: AC, AA; Supervision: AA.

Data availability The material used in this article is deposited in the collection of the Natural Sciences Museum of Granollers (Barcelona, Spain). The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethical approval Not applicable.

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest. The authors have no competing interests to declare that are relevant to the content of this article. No funding was received to assist with the preparation of this manuscript.

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