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Comparative morphological analysis of yellow-legged hornet (*Vespa velutina nigrithorax*) and European hornet (*Vespa crabro*) based on modern imaging techniques

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Introduction: The yellow-legged hornet (*Vespa velutina nigrithorax* Lepeletier, 1836) and the European hornet (*Vespa crabro* L., 1758) are two social generalist predator wasps that have successfully expanded beyond their native ranges, raising ecological concerns in newly colonized regions. This study presents a comparative analysis of the two species based on morphological parameters derived from digital microscopy and micro-CT imaging.

Methods: Species were collected in Hungary and examined in order to assess differences in body size, colouration, and flight-related morphology. To determine the differences between species, 16 different morphological parameters were measured by micro-ct examination and digital microscopy. The flight parameters of the examined two species were assessed through 14 flight-related coefficients and a correlation matrix and a linear model based on these.

Results and discussion: Results from the colour analyses performed significantly darker colouration of *V. v. nigrithorax* compared with *V. crabro*. Morphological measurements confirmed that *V. crabro* is generally larger and more robust in body size, while *V. v. nigrithorax* possesses relatively longer legs and a greater wing surface area proportional to body mass. *V. v. nigrithorax* outperformed *V. crabro* in most flight-related traits, e.g. speed, manoeuvrability, balancing ability, hovering and carrying capacity. Correlation analyses supported these findings, showing stronger associations among wing parameters in *V. v. nigrithorax* and more uniform body-thorax interaction and more robust body structure in *V. crabro*. These results argue that *V. v. nigrithorax*'s better flight performance underlies its effective bee-hawking behaviour and competitive dominance in

habitats in which the two hornet species co-occur. The study highlights how morphological adaptations contribute to predatory success and invasion potential. Our findings also confirm that in the absence of natural enemies, an adventive predator can exhibit significant ecological advantages in competitive interactions, certainly in the initial success of an invasive species.

KEYWORDS

colourization, comparative morphology, external morphology, flight abilities, general predators

1 Introduction

The yellow-legged hornet (*Vespa velutina nigrithorax* Lepeletier, 1836) (Hym.: Vespidae) and the European hornet (*Vespa crabro* L., 1758) (Hym.: Vespidae) occupy different geographic ranges with different native fauna. As top insect predators, these two *Vespa* species have successfully established non-native populations far from their endemic ranges, adding to economic difficulties and environmental problems (Beggs et al., 2011; Barbet-Massin et al., 2020). Both are invasive species that permanently occupy new habitats with negative consequences for the natural environment and/or humans (Monceau et al., 2015; Otis et al., 2023). The natural range of *V. crabro* is temperate Eurasia, from the United Kingdom through the Iberian and Italian Peninsula to the Far East, Eastern Russia and Japan. It was accidentally introduced into eastern North America in the 1840s (Bequaert, 1932; Shaw and Weidhaas, 1956; Landolt et al., 2010; Bass et al., 2022). One of the most devastating enemies of the western honey bee (*Apis mellifera* L., 1758) (Hym.: Apidae), the yellow-legged hornet is currently spreading rapidly and become the most abundant *Vespa* species in the world (Park et al., 2024). *V. v. nigrithorax* is widely distributed and occupies different habitats in tropical and subtropical regions of Asia, from Pakistan throughout most of Indochina, Indonesia, and Taiwan, Southeastern Asia and the Malay Peninsula and to North America (Choi et al., 2012; Monceau et al., 2014; Liroy et al., 2023; Otis et al., 2023; Hoebeke et al., 2024). Its high invasion potential has been demonstrated by its rapid dispersal through Europe, Korea, and Japan (Robinet et al., 2017; Liroy et al., 2023; Otis et al., 2023).

The emergence and successful spread of this invasive hornet into new habitats poses a serious threat to the conservation of the native insect fauna, due to their predation and competition abilities (Snyder and Evans, 2006; Cini et al., 2018; Carisio et al., 2022). The competitive interactions can emerge among *Vespa* species when their habitats overlap within the same biotope. This phenomenon relates to several factors, such as overlapping nesting sites, access to resources, prey acquisition, and partially overlapping seasonal phenology (Beggs et al., 2011; Barbet-Massin et al., 2020). Each species efficiently exploits the organic resources available in its endemic range, thereby effectively occupying its ecological niche

(Landolt et al., 2010; Liroy et al., 2023). However, this ecological success has also facilitated the colonization of new, previously uninhabited environments, driven by factors such as increased transportation, urbanization, and, importantly, climate change. *V. crabro* has historically occupied Eurasian regions (Bequaert, 1932; Shaw and Weidhaas, 1956; Snyder and Evans, 2006; Landolt et al., 2010). Whilst *V. crabro* is a generalist predator, it has not been reported to cause significant losses of honey bees, or environmental damages within endemic nor newly introduced ranges (Cini et al., 2018; Rome et al., 2021). The yellow-legged hornet by way of contrast has a semi-specialised diet which mainly targets honey bees and social wasps of the genus of *Vespula* and *Polistes*, and Diptera species (Laurino et al., 2019; Rome et al., 2021). Its presence in regions it has invaded raises various problems, due to its high predation of *A. mellifera*, causing a serious economic challenge for the beekeeping industry (Monceau et al., 2014; Rome et al., 2021; Diéguez-Antón et al., 2025).

The competition between predator and prey is an ongoing evolutionary contest, enacted via traits and strategies that evolve to maximize the chances of the predator to successfully catching food resources, and for local prey populations survive the attack and live on (Brodie and Brodie, 1999; Kwon and Choi, 2020). The problematic situation could arise when the ranges of two *Vespa* species begin to overlap. In such cases, the native *Vespa* species may experience competitive pressures, or even displacement following the arrival of a previously absent *Vespa* species (Snyder and Evans, 2006; Cini et al., 2018; Carisio et al., 2022; Liroy et al., 2023). However, in areas where the endemic species coexists with the ecologically similar and invasive *V. v. nigrithorax*, its dominance may be challenged. Previous studies have shown that *V. v. nigrithorax* can compete with other *Vespa* species within its invasive range in Asia (Choi et al., 2012; Park et al., 2024). Moreover, it has rapidly become the most common hornet species in Korea near Busan within six years (Choi et al., 2012; Liroy et al., 2023; Park et al., 2024).

In Europe, competition has also been hypothesized between *V. v. nigrithorax* and the native *V. crabro*, although direct field-based confirmation remains limited (Cini et al., 2018; Carisio et al., 2022). There are clearly visible morphological differences between the workers of the *Vespa* species studied for, example in terms of

colour and body size (Kovac and Stabentheiner, 2012; Smith-Pardo et al., 2020; Do et al., 2022; Mattila et al., 2022). These differences are the result of adaptive processes and predation strategy linked to the biotope of the original habitat (Araújo et al., 2004; Perrard et al., 2013, 2016). Among hornet species, the flight capacity is a major driver of success, most exemplified by bee-hawking activity, a specialised predation strategy found in the case of *V. v. nigrithorax* (Tan et al., 2007; Sauvard et al., 2018; Cappa et al., 2021).

The morphology associated with flight affects various aspects of performance, such as lifting capacity, speed, endurance, and manoeuvrability (which refers to the ability to change the velocity and the direction of movement) (Marden, 1987; Sauvard et al., 2018). Several morphological parameters and the ratios calculated from them can be used to infer flight performance and locomotion ability (Marden, 1987; Byrne et al., 1988; Danforth, 1989; Sauvard et al., 2018; Kwon and Choi, 2020). There is currently a scarcity of data on insect morphological characteristics derived from three-dimensional micro-CT imaging (Jonsson, 2023; Toulkeridou et al., 2023). Overall, relatively few studies in entomology have employed non-invasive imaging techniques such as micro-tomography to investigate insect anatomy. The principal advantage of this technique lies in its ability to capture detailed, comparable internal structures and morphological features without resorting to dissection or other destructive methods, thus preserving specimens in their natural state (Jonsson, 2023; Moraes et al., 2023; Toulkeridou et al., 2023).

Based on these morphological features, our present research aimed to investigate the fundamental differences in the body structure of the two *Vespa* species, *V. crabro* and the invasive *V. velutina nigrithorax*, to understand and describe the external morphology in more detail, and to compare the two species flying abilities by calculating several flight coefficient factors. Our work also aimed to confirm the differences in morphology related to hunting strategies of the two species using modern 3-D imaging techniques and digital microscopy. Using these data, it is possible to compare the predation success and ecological competitiveness of two generalist predators within a specific habitat by examining their morphological traits. By introducing a generalist predator into a newly occupied habitat, the study can effectively highlight the strengths and weaknesses of this predator when competing with endemic species, providing valuable insights into ecological adaptations and competitive interactions.

2 Materials and methods

2.1 Sampling

Worker hornets of the two test species were collected from Hungary on 5th of October 2023. Specimens of *V. v. nigrithorax* represented workers from a colony detected for the first time in Hungary, originating from Kimle (Győr-Moson-Sopron County; GPS: 47°49'38.3"N; 17°22'17.9"E). To eliminate possible variation that the external factors cause in the developmental stage of a nest, *V. crabro* workers from one colony were collected at the same time

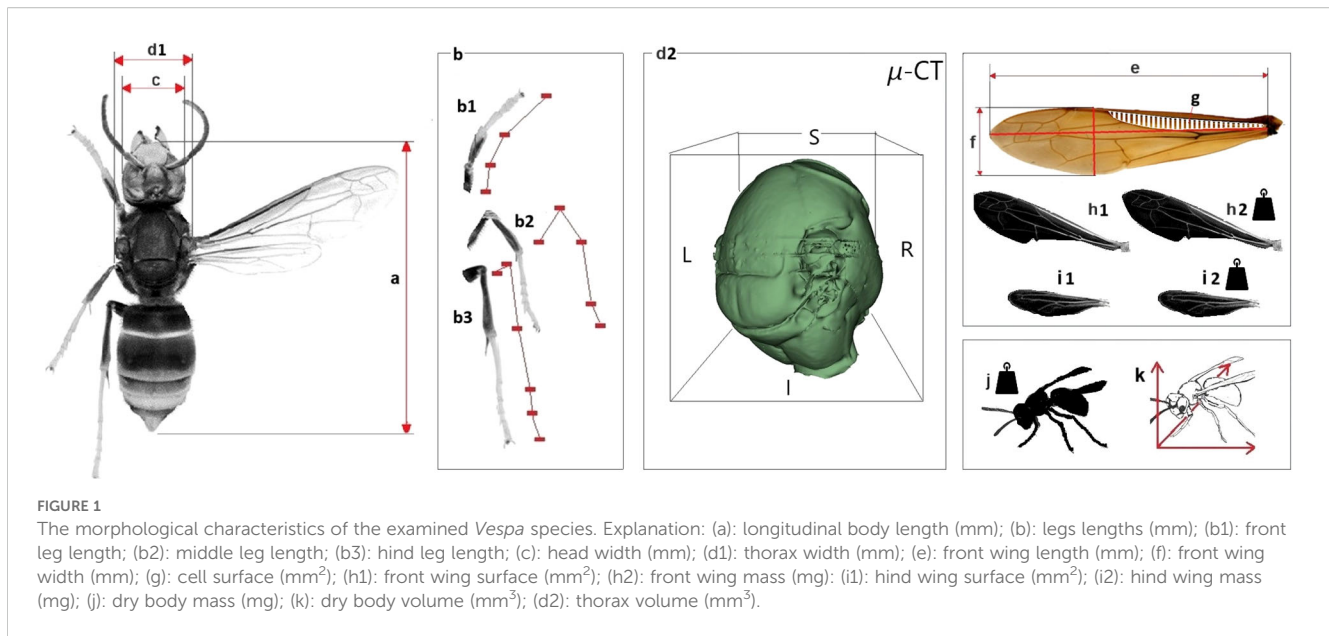
in Kimle (Győr-Moson-Sopron County; GPS: 47°49'43.0"N; 17°22'08.7"E). Insects were trapped with insect nets and immediately killed with ethyl acetate vapour. The collected insect material was stored in a laboratory under room-temperature conditions until the studies were begun. In order to compare the morphological characteristics of *V. crabro* and *V. v. nigrithorax*, the whole body and wing compartments were analysed. All investigated parameters were represented by averages of values taken from 15 individuals of each species, a sample size considered adequate in terms of species representation because of the fact that these insects have a haplodiploid breeding system and hence tend to be somewhat inbred anyway, and in the case of the invasive hornet here studied, populations probably initially derived from a few mated founder queens (Taylor et al., 2024). For the micro-CT imaging and for the wing parameters analysis air-dried pinned insects were used. The insects were pinned using a 0.2 mm metal needle and mounted on a polystyrene tray following the method described by Methven et al. (1995). Before pinning, wings were carefully removed from each specimen and mounted on microscope slides with Euparal mounting media to allow subsequent wing measurements.

2.2 Micro-computed tomographical analysis

A Nikon XT H 225 ST X-Ray Tomograph instrument was applied to perform the micro-CT scans. During the measurements, 160 kV accelerating voltage, and 85 µA beam current were used. For the scan, 1,250 projections were acquired with 2 frames/projection, which meant ~17 GB file size. The effective pixel size was 8 µm. During the reconstruction, scatter reduction, noise reduction, median filter, and image processing were applied to enhance the quality of the scans. The analysis was performed using Volume Graphics Studio Max 2023/1 software. The measurements were performed on prepared wasps that had been air-dried. Consequently, very thin layer thicknesses were formed, which made measurements difficult. Additionally, a thin metal needle used for fixation of the insects gave a high contrast, which caused a certain amount of shading. To eliminate this, several software algorithms were applied to reduce the shadowing and enhance the contrast. The measurements were performed both automatically and manually using Volume Graphics Studio Max 2023/1 and 3D Slicer software (version 5.6.3).

2.3 Morphometric measurements

Measurements of morphological parameters of the 15 individuals of each species were conducted using digital microscopy and micro-CT imaging techniques. A summary of the measured parameters is presented in Figure 1. Microscopic examinations were performed using a Keyence VHX-XF1 digital microscope equipped with a VH-Z20T lens (magnification range: 20× to 200×). Morphometric analyses were performed on dissected



forewings and hindwings, including measurements of front wing length (e), front wing width (f), and cell surface area (g). Additionally, the total surface areas of the front wings (h1) and hind wings (h2) were determined according to the abbreviations detailed in Figure 1. To evaluate the flight capabilities and consequent predatory specializations of the examined *Vespa* species, various morphological parameters were measured using micro-CT imaging and analysed in 3D Slicer software (version 5.6.3). Volume measurements – specifically, dry body volume (k) and thorax volume (d2) – were calculated using the Segment Editor and Segment Statistics modules. Additionally, linear dimensions including longitudinal body length (a), leg lengths (b), head width (c), and thorax width (d1) were measured utilizing the Markups module within 3D Slicer.

The mass of various body components, including front wing mass (h2), hind wing mass (i2), and dry body mass (j), was measured using an Ohaus Explorer Semi-Micro balance (model EX125), with a precision of 0.01 mg.

To compare the estimated flight capabilities of the two species and thus estimate their hunting abilities, specific flight-related morphological ratios were calculated. The morphological parameters outlined in Figure 1 contributed to the calculation of these ratios listed in Table 1. The formulas for each ratio, along with the specific flight abilities they directly influence, are presented in Table 1.

2.4 Colour analysis

The MultiSpec (Version 2024.05.16 64-bit Windows) software (Biehl and Landgrebe, 2002) was used to classify different images from frontal and dorsal perspectives of each species (n=15) taken by Keyence VHX-XF1 digital microscope equipped with a VH-Z20T lens. For the precise classification of the species this was preformed by taking samples from certain parts of the images and assigned

them to three different classes (bright, reddish-brown, black). The coverage values of each classes were used for the differentiation of the species. The classification was done by selecting a small group of pixels from the different body parts (eg. clypeus), which is a dataset that represents the characteristics of the specified class. If an image fragment contained multiple colour tones, it was sampled in its entirety, thus minimizing the problem caused by unclassified pixels. For the classification of five samples from the image for a given class, this was done to increase the accuracy of the analysis process. The classification was performed using the Gaussian Maximum Likelihood classification algorithm. After the classification were performed, the individual classes were displayed in different colours, the image accuracy of the analysis being measured by Kappa statistics.

2.5 Data evaluation and statistical analysis

Shapiro-Wilk normality test was conducted on the dataset of colour analysis, morphological measurements and calculated parameters. The colour, morphological and calculated parameters of the two *Vespa* species examined were evaluated using one-way ANOVA ($p < 0.05$). The relationship between the morphological parameters were calculated by the Pearson-Correlation Matrix for each species and visualized on a heat map. To analyse the hunting and flight performances of each species, a linear model was created for the scoring of different calculated parameters. Given the multiple parameters that were considered in the characterisation of each skill (scouting, hunting, prey carrying as shown in Figure 2), a scoring method was developed that encompassed all the derived parameters. It was hypothesised that all the parameters presented in Figure 2, whether they influenced the flight, hunting or prey-catching properties of the species in a positive or negative direction, were considered with similar weighting. The scoring method was based on a normalisation procedure, i.e. firstly all

TABLE 1 The calculated morphometric coefficients used to estimate flight and predation characteristics of the examined two *Vespa* species.

No.	Abbreviation of ratio	Name of ratio	Calculation of ratio	A consequent skill	References
Leg-derived abilities					
1.	RFL	relative front leg length	$a/b1$	prey capture	Dudley, 2002; Burnett and Combes, 2023
2.	RML	relative middle leg length	$a/b2$	prey capture, manoeuvre, flight balance	Dudley, 2002; Burnett and Combes, 2023
3.	RHL	relative hind leg length	$a/b3$	aerodynamics, flight balance	Dudley, 2002; Burnett and Combes, 2023
Wing-derived abilities					
4.	FWQ	front wing quotient	e/f	flight speed, manoeuvrability, pursuit ability, hovering, capturing	Byrne et al., 1988; Dudley, 2002
5.	WL	wing loading	$j/(h1+i1)$	speed, manoeuvrability, pursuit ability, hovering, lifting ability, carrying ability	Byrne et al., 1988; Dudley, 2002
6.	FWD	front wing density	$h2/h1$	speed, pursuit ability, hovering	San Ha et al., 2013
7.	HWD	hind wing density	$i2/i1$	speed, pursuit ability, hovering	San Ha et al., 2013
8.	RFS	relative front wing stability	$h1/g$	hovering, lifting and carrying ability	Byrne et al., 1988
9.	RWS	relative total wing surface	$(h1+i1)*2/j$	speed, pursuit ability, hovering, lifting ability, carrying ability	Araújo et al., 2004
10.	Buoy.A	buoyancy ability	$(h1+i1)/(j/k)$	hovering, lifting ability, carrying ability	Dudley, 2002
Body-derived abilities					
11.	RTS	relative thorax size	d/c	capturing, carrying ability	Byrne et al., 1988
12.	RTV	relative thorax volume	$d2/k$	capturing, lifting ability, carrying ability	Dudley, 2002
13.	BD	body density	j/k	manoeuvrability, hovering, pursuit ability, capturing	Dudley, 2002
14.	SDS	shape depending speed	$d2/a$	speed, manoeuvrability, pursuit ability	Dudley, 2002

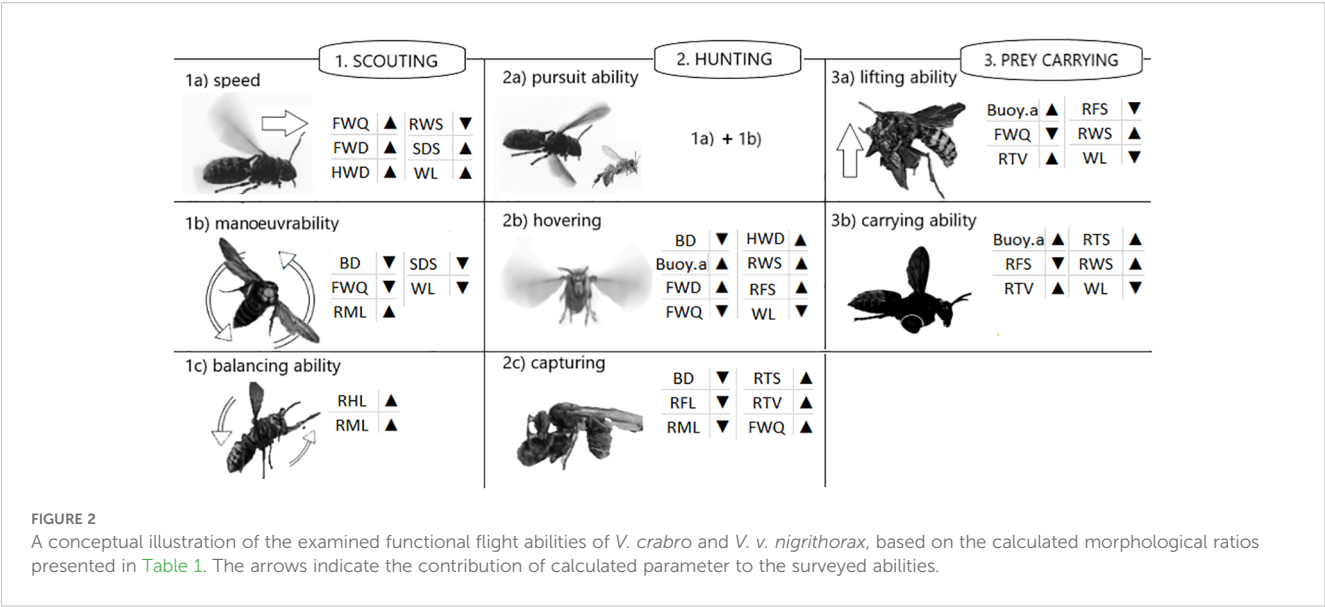
data were sorted in ascending order of value, then the minimum value was invariably associated with 0 and the maximum value with 1, and a linear equation of a Descartes coordinate was plotted between the two points. Subsequently, all derived parameters were converted to a number ranging from 0 to 1 and aggregated as illustrated in Figure 2. The upward-pointing arrow was interpreted as a positive value, the downward one as a negative value. The scoring of different flight abilities was based on Figure 2. Statistical analyses were performed using Microsoft Excel (Office version 2016) and R statistics software version 4.2.1 (Team, 2010)

applying the ‘corrplot’ (Wei and Simko, 2017) and ‘ggplot2’ packages (Wickham, 2016).

3 Results

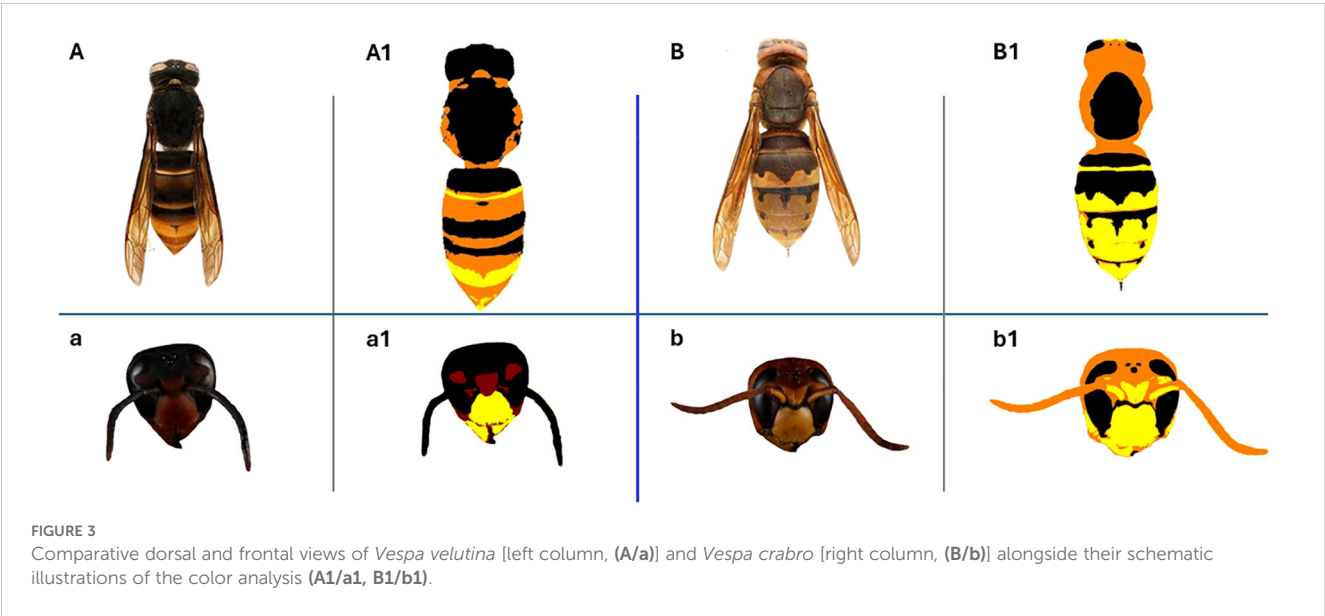
3.1 Colour analysis

Based on analyses conducted to assess interspecific differences in colouration, various body regions were taken into consideration,



the colour analysis results of one specimen of each species illustrated in Figure 3. Regarding head colouration viewed from the front, the following distinctions were observed between the two species. In *V. crabro*, brownish-reddish colouration dominated, covering $44 \pm 0.5\%$ of the head, while in *V. v. nigrithorax*, the brownish-reddish colouration averaged $18 \pm 0.5\%$. This difference was statistically significant ($df = 1$; $F = 19398$; $p < 0.001$). Bright yellow tones were dominant in *V. crabro*, covering $30 \pm 0.4\%$ of the head, in contrast to *V. v. nigrithorax*, where the head was covered by bright yellow colouration at a rate of $22 \pm 0.8\%$. Statistical analysis confirmed the difference ($df = 1$; $F = 1173$; $p < 0.001$). Regarding black colouration, the head of *V. crabro* exhibited an average of $26 \pm 0.5\%$ such coverage, while *V. v. nigrithorax* showed an exceptionally high black colouration at $59 \pm 1.1\%$. This disparity was also statistically significant ($df = 1$; $F = 10622$; $p < 0.001$). The Kappa

statistics values were 98.8% for *V. crabro*, 98.6% for *V. v. nigrithorax*. In dorsal view, similar trends were observed in terms of colouration. In *V. crabro*, brownish-reddish tones dominated the back, accounting for $41 \pm 1\%$, compared to $34 \pm 0.5\%$ in *V. v. nigrithorax*. The difference between the species was statistically significant ($df = 1$; $F = 564$; $p < 0.001$). Noteworthy differences were found in the yellow colouration, where *V. crabro* exhibited a value similar to that of the head ($31 \pm 1\%$), whereas *V. v. nigrithorax* showed a significantly lower average coverage of $10 \pm 0.5\%$. This difference in yellow coverage on the dorsal surface was confirmed through one-way ANOVA ($df = 1$; $F = 6129$; $p < 0.001$). Concerning black colouration, *V. crabro* had $28 \pm 0.6\%$ of the back-coloured black, while *V. v. nigrithorax* displayed the highest level of black colouration at $56 \pm 0.6\%$. The interspecific differences in black



colouration on the back were statistically significant ($df = 1$; $F = 18568$; $p < 0.001$). The Kappa statistics values of the dorsal view were high for the examined species 98,5 for *V. crabro* and 98,7% for *V. v. nigrithorax*.

3.2 Body morphological analyses

The analysis of body size measurements revealed that *V. crabro* exhibited larger values across all measured parameters and dimensions compared to *V. v. nigrithorax*. Furthermore, all measured values were found to differ significantly between the two species. The mean values, standard deviations of the measured parameters, and the results of the statistical analyses are presented in Table 2. The differences between the two species can best be determined from the numbered morphological quotients. The mean values, standard deviations of the calculated morphometric coefficients, and the results of the statistical analyses are presented in Table 3.

3.2.1 Leg-derived parameters

In the case of relative front leg length (RFL) we found no significant differences ($df=1$; $F=3.2$; $p=0.090$), both *V. crabro* and *V. v. nigrithorax* having similar front leg proportions relative to body length. However, a significant difference was calculated in the case of relative middle leg length (RML) ($df=1$; $F= 14.5$; $p=0.001$). According to the coefficient, *V. v. nigrithorax* has proportionally shorter middle legs relative to body length compared to *V. crabro*.

Interestingly, both species have similar parameters derived from the hind leg length (RHL) ($df=1$; $F=0.2$; $p=0,676$).

3.2.2 Wing-derived parameters

Regarding the front wing quotient (FWQ), a highly significant difference was observed ($df=1$; $F=40.1$; $p<0.001$). The higher value in FWQ indicates relatively narrower wings of *V. v. nigrithorax*. The wing loading (WL) was significantly different, as supported by statistical analysis ($df=1$; $F=18.1$; $p<0.001$). A more robust body structure in *V. crabro* is indicated by its elevated wing loading, as demonstrated in Table 2. Statistically significant differences were found in front wing density (FWD) ($df=1$; $F=74.3$; $p=0.001$) and hind wing density (HWD) ($df=1$; $F=117.8$; $p=0.002$), with *V. v. nigrithorax* exhibiting higher values in both cases. Interestingly, relative front wing stability (RFS) did not differ significantly between the species ($df=1$; $F=1.1$; $p=0.314$), suggesting similar wing stability. The relatively larger wings of *V. v. nigrithorax*, in proportion to its body mass, were reflected in the relative total wing surface (RWS), which showed a statistically significant difference between the species ($df=1$; $F=19.2$; $p<0.001$). It is noteworthy that a similar buoyancy number reflects comparable load-carrying abilities of the examined species, supported by the analysis ($df=1$; $F=1.8$; $p=0.201$).

3.2.3 Body-derived parameters

The relatively robust body structure of *V. crabro* can be indicated by the higherr value of relative thorax size (RTS), which was different for the two species ($df=1$; $F=12.9$; $p=0.002$). Curiously,

TABLE 2 The measured morphological parameters of *Vespa crabro* and *Vespa velutina nigrithorax*, and the findings from statistical analysis.

Measured parameter	Mean value		One-way ANOVA		
	<i>Vespa crabro</i>	<i>Vespa velutina</i>	<i>p</i> -value	<i>df</i>	<i>F</i>
Dry body weight (mg)	178 ± 23	124 ± 15	< 0.001	1	39.9
Front wing weight (mg)	1.1 ± 0.1	1.0 ± 0.08	0.014	1	7.5
Hind wing weight (mg)	0.30 ± 0.03	0.27 ± 0.03	0.026	1	5.9
Front leg length (mm)	16.4 ± 0.3	15.1 ± 0.4	< 0.001	1	66.2
Middle leg length (mm)	18.4 ± 0.5	16.4 ± .0.6	< 0.001	1	66.7
Hind leg length (mm)	22.1 ± 0.5	21 ± 0.7	< 0.001	1	18.3
Body length (mm)	20.8 ± 1.2	19.8 ± 1.4	0.020	1	6.6
Head width (mm)	5.7 ± 0.1	5.4 ± 0.2	< 0.001	1	21.9
Thorax width (mm)	6.2 ± 0.1	5.7 ± 0.3	< 0.001	1	33.8
Body volume (mm ³)	513 ± 45	420 ± 38	< 0.001	1	24.6
Thorax volume (mm ³)	173 ± 14	142 ± 14	< 0.001	1	26.1
Wing length (mm)	18.8 ± 0.7	18 ± 0.7	0.017	1	6.9
Wing width (mm)	5.4 ± 0.2	4.8 ± 0.2	< 0.001	1	46.2
Cell surface (mm ²)	8.2 ± 0.6	7 ± 0.6	< 0.001	1	20
Front wing surface (mm ²)	69.8 ± 5.2	60 ± 4.6	< 0.001	1	19.9
Hind wing surface (mm ²)	26.5 ± 1.1	19.5 ± 1.8	< 0.001	1	108.2

TABLE 3 The calculated morphometric coefficients of *Vespa crabro* and *Vespa velutina nigrithorax* and the statistical analysis outcomes.

Measured parameter	Mean value		One-way ANOVA		
	<i>Vespa crabro</i>	<i>Vespa velutina</i>	<i>p</i> -value	df	F
RML	1.13 ± 0.05	1.21 ± 0.03	0.001	1	14.482
FWQ	3.49 ± 0.09	3.71 ± 0.06	< 0.001	1	40.134
WL	1.84 ± 0.15	1.55 ± .0.15	< 0.001	1	18.122
FWD	0.016	0.017	< 0.001	1	74.237
HWD	0.011	0.014	0.002	1	117.773
RWS	1.09 ± 0.09	1.29 ± 0.12	< 0.001	1	19.201
RWM	0.016 ± 0.001	0.021 ± 0.001	< 0.001	1	42.573
RTS	27.56 ± 1.57	25.03 ± 1.6	0.002	1	12.922
BD	0.346 ± 0.015	0.294 ± 0.009	< 0.001	1	85.830
SDS	8.31 ± 0.21	7.15 ± 0.57	< 0.001	1	36.387

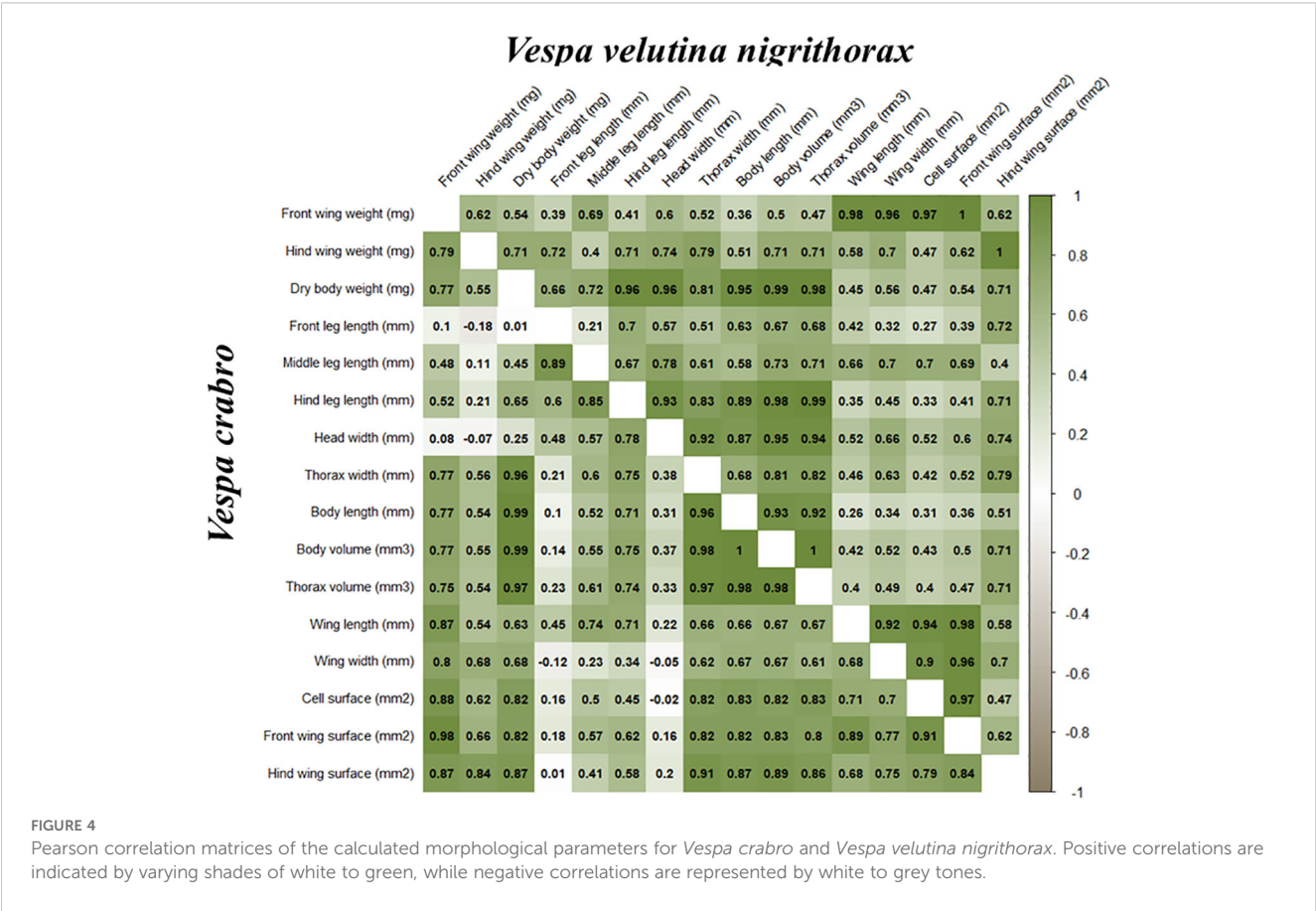
the relative thorax volume (RTV) was alike in both species, indicating similar proportions of thorax-to-body volume (df=1; F=0.1; *p*=0.797). Body density (BD) (df=1; F= 85.84; *p*=0.001) and shape-dependent speed (SDS) (df=1; F= 36.4; *p*=0.002) were also elevated in *V. v. nigrithorax*, like RTS pointing to a more robust body structure.

3.3 Association between morphometric parameters

The Paired-Pearson correlation analysis illustrates on Figure 4 the strength and direction of relationships among the measured morphometric parameters of *V. crabro* and *V. v. nigrithorax*. The parameters include body dimensions (dry body weight, body volume, body length, head width, thorax width, thorax volume) leg metrics (front, middle, hind leg lengths) and wing dimensions (length of front wing, width of front wing, front and hind wing surface and weight, front wing cell surface) summarized in Table 2. The analysis reveals the correlation coefficient to be higher than 0.5 and to include the weak (0–0.499) moderate (0.5–0.599), strong (0.6–0.799) and very strong (0.8–1.00) relationships as well as the negative relationships.

3.3.1 Correlation patterns in *Vespa crabro*

Regarding body dimensions, dry body weight exhibits very strong positive correlations with body volume (*r*=0.99), body length (*r*=0.99), thorax width (*r*=0.96), and thorax volume (*r*=0.97). Additionally, correlations between dry body weight and wing surface parameters are strong, with correlation coefficients ranging from 0.82 to 0.87. Body length, thorax width, thorax volume, and body volume parameters demonstrate very strong correlations (*r* ranging from 0.96 to 1). Body and thorax dimensions also correlate very strongly with wing surface parameters (*r* ranging from 0.80 to 0.91). However, head width correlations are relatively weak, showing both low positive and negative



relationships (r ranging from -0.15 to 0.38) between all parameters, except the moderate correlation with front leg length ($r=0.48$).

Wing-related dimensions display very strong correlations; wing length strongly correlates with front wing weight ($r=0.87$), front wing surface area ($r=0.89$), and wing cell surface area ($r=0.91$). Additionally, front and hind wing surface parameters are highly correlated ($r=0.84$). Both front and hind wing surfaces show very strong correlations with their respective wing weights (r ranging from 0.80 to 0.88). The front wing weight correlates strongly with most body dimensions (r ranging from 0.75 to 0.77), except for a weak correlation observed with head width ($r=0.08$). Hind wing weight demonstrates moderate correlations with body metrics (r ranging from 0.54 to 0.56).

Leg-length parameters reveal moderate to strong positive correlations with overall body size and weight metrics, particularly middle and hind leg lengths (r ranging from 0.52 to 0.78). However, front leg length correlations are relatively weak, showing both low positive and negative relationships, exemplified by a notably weak negative correlation between front leg length and hind wing weight ($r=-0.18$), except for the moderate correlations with head width ($r=0.48$) and wing length ($r=0.46$).

3.3.2 Correlation patterns in *Vespa velutina nigrithorax*

Dry body weight exhibits very strong positive correlations with body volume ($r=0.99$), thorax volume ($r=0.98$), thorax width ($r=0.81$), and body length ($r=0.95$). Correlations between dry body weight and wing surface parameters (front wing surface, hind wing surface, and cell surface area) range from moderate to strong (r ranging from 0.47 to 0.71). Interestingly, correlations between body length, body width, and body surface parameters with wing length, wing width, and wing surface parameters range from weak to strong (r ranging from 0.26 to 0.79). The weakest correlation was observed between body length and wing length ($r=0.26$), contrasting sharply with the very strong relationship between body length and body volume ($r=0.93$). Furthermore, body volume, thorax volume, head width, and thorax width parameters are all very strongly intercorrelated (r ranging from 0.81 to 1). The correlations between body and thoracic parameters and wing surface dimensions range from weak to strong (r ranging from 0.40 to 0.71).

Wing dimensions display consistently strong correlations. Specifically, front wing weight correlates very strongly with front wing length ($r=0.98$), wing width ($r=0.92$), front wing surface ($r = 1.00$), and cell surface area ($r=0.96$). Additionally, front and hind wing surface parameters are moderately correlated ($r=0.62$). Hind wing parameters exhibit weak to strong correlations with front wing length, width, and cell surface area (r ranging from 0.47 to 0.70).

Leg-length parameters reveal considerable variability in their correlations. Front and hind leg lengths exhibit a strong correlation with each other ($r=0.70$), whereas front and middle leg lengths demonstrate only a weak correlation ($r=0.21$). Overall, leg-length parameters show strong positive correlations with body dimensions, particularly hind leg length, which strongly correlates with body weight, width, and volume parameters (r ranging from 0.83 to 0.96). Middle leg length correlations with body dimensions are moderate to strong (r ranging from 0.58 to 0.78). Moreover, a descending correlation trend like that observed in *V. crabro* is apparent, with front leg length

showing moderate to strong correlations with body metrics (r ranging from 0.51 to 0.67). Correlations between front and hind leg lengths and wing dimensions are weak (r ranging from 0.27 to 0.45), except for a strong correlation with hind wing weight ($r=0.71$). Lastly, middle leg length correlates strongly with wing dimensions (r ranging from 0.66 to 0.70), but weakly with hind wing weight ($r=0.40$).

3.4 Linear model of flight and hunting abilities

Based on the results of the linear model (Table 4), we show how in ways that likely influence flight abilities are reflected in the scores produced by the model. In terms of scouting abilities, *V. v. nigrithorax* markedly outperformed *V. crabro*. Regarding flight speed, *V. v. nigrithorax* achieved an average score of 2.64 , while *V. crabro* reached a lower score of 2.14 . In terms of manoeuvrability, *V. crabro* performed notably worse, with an average score of -2.19 . Although *V. v. nigrithorax* also received a negative value -0.8 , its performance was better in this aspect. Furthermore, *V. v. nigrithorax* demonstrated more balanced flight with an average score of 1.25 , compared to 0.81 achieved by *V. crabro*.

In the context of abilities contributing to hunting performance, pursuit ability was based on flight speed and manoeuvrability. *V. v. nigrithorax* outperformed *V. crabro* in both of these underlying traits, whilst the same trend was also observed in the case of pursuit ability. *V. v. nigrithorax* achieved a higher scoring of 1.85 in opposition to -0.05 . The analysis revealed substantial differences in hovering ability, with *V. v. nigrithorax* achieving a significantly higher score of 2.27 in the linear model, compared to a score for *V. crabro* of 0.21 . The results for prey capturing ability showed unexpected tendencies, although the differences were minor; *V. crabro* attained a slightly better score -0.07 than *V. v. nigrithorax* -0.11 . Nevertheless, these values remained relatively close, indicating only a marginal difference between the two species.

TABLE 4 Comparative functional flight ability scores of *Vespa v. nigrithorax* and *Vespa crabro* based on a linear model and the calculated flight related coefficients.

Scouting	<i>V. velutina</i>	<i>V. crabro</i>
Speed	2.64	2.14
Manoeuvrability	-0.79	-2.19
Balancing ability	1.25	0.81
Hunting	<i>V. velutina</i>	<i>V. crabro</i>
Pursuit ability	1.85	-0.05
Hovering	2.27	0.21
Capturing	-0.11	-0.07
Prey carrying	<i>V. velutina</i>	<i>V. crabro</i>
Lifting ability	0.18	0.07
Carrying ability	1.27	1.1

The greater among the two species are in red.

In aerial predatory social insects, the ability to transport prey for the benefit of the colony is essential. For the calculation of flight related scores, we incorporated coefficients associated with thorax structure and flight capabilities. The analyzed parameters revealed only minor differences between the two species. Regarding lifting ability, *V. v. nigrithorax* slightly outperformed *V. crabro*, achieving a score of 0.18 compared to 0.07. When assessing the ability to simulate prey transport, the differences became more pronounced, with *V. v. nigrithorax* displaying a higher value of 1.27 compared to *V. crabro* of 1.1.

4 Discussion

The paradox of the *Vespa* genus lies in the fact that its various species are highly successful organisms within their respective native habitats, whereas in our case, both examined species have successfully colonized various regions (Monceau et al., 2015; Otis et al., 2023; Hoebeke et al., 2024). The different endemic ranges of these two species may be reflected in the very distinct colouration patterns shown, from both the frontal and dorsal views (Kovac and Stabentheiner, 2012; Do et al., 2022; Mattila et al., 2022). Our study confirmed that the dorsal colouration of *V. v. nigrithorax* dorsal colouration is much darker (9.5% bright; 34.3% reddish-brown; 56.2% black) than that of *V. crabro*, suggesting that darker colour may relate to thermal regulation, crypsis, or mimicry (Joron, 2009; Perrard et al., 2014). Furthermore, the colouration of *V. crabro* displays a more vivid and variegated dorsal tone (30.9% yellow; 41% reddish brown; 28.1% black) with more bright yellowish colours, which may well serve as aposematic signalling against predators (Joron, 2009; Perrard et al., 2014). The different colouration in different areas may certainly play a role in terms of the ecological specialization and hence success of the two species. In the eastern Palaearctic, within its native range, *V. v. nigrithorax* does not appear to have any natural predators that exert significant population-regulating pressure. In contrast, within the western Palaearctic, the European bee-eater (*Merops apiaster*; L. 1758) (Aves: Meropidae), which feeds on hymenopterans, including bees and wasps, has been identified as a potential natural enemy of *V. v. nigrithorax* (Onofre et al., 2023). Moreover, the cryptic black colouration of *V. v. nigrithorax* may, in some cases, effectively conceal it from visual predators, thereby reducing its likelihood of being preyed upon (Endler, 1988; Keszthelyi et al., 2024).

The fighting ability related to the success of a predator is largely influenced by body size (Kwon and Choi, 2020). Some earlier studies support the differences here found between the examined two *Vespa* species, including in terms of morphological and behavioural aspects. Thus, our results reinforce the study by Kwon and Choi (2020), completed using deeper morphological analyses. In our study *V. crabro* was here found to be larger than *V. v. nigrithorax* in every aspect, mostly the body volume and dry body weight, reflecting the clearly visible different anatomical structure. The correlation analysis revealed more structural differences in the body anatomy, while *V. crabro* displayed more uniformly strong correlations among body and thoracic parameters, suggesting a more robust body structure. In contrast, *V. v. nigrithorax* exhibited stronger correlations among wing traits and leg traits suggesting the key to the success of this species is

related to its flight performance. The different body structure can be rooted in terms of direct ecological pressure, thereby supporting the results of Kwon and Choi (2020) in suggesting that *V. v. nigrithorax* tends to avoid direct competition (fighting, nesting sites) with native hornet species including *V. crabro* in its Asian range.

The predatory success of these two social wasp species is fundamentally based not only in their overall body size but in their flight performance capabilities (Tan et al., 2007; Sauvard et al., 2018; Cappa et al., 2021). To gain a deeper understanding of the structural differences between *V. crabro* and *V. v. nigrithorax*, and thereby their potential predatory success, we calculated multiple flight-related morphological ratios, analyzing them through the linear model developed specifically to assess key differences of flight and predation abilities.

Based on the analysed coefficients, *V. v. nigrithorax* has relatively longer legs in proportion to its body size, which likely supports enhanced aerial balance and prey-capturing ability (Dudley, 2002; Burnett and Combes, 2023). In contrast, *V. crabro* showed higher values in buoyancy-ability but not significant different to that of *V. v. nigrithorax* in terms of the relative thorax size and volume. However, in terms of wing loading and wing surface-to-body ratio, *V. v. nigrithorax* appears more adapted for hovering flight and rapid manoeuvrability. The higher wing surface, density, and shape related quotients emphasize the better flight performances of *V. v. nigrithorax* that appear unequivocally reflected in different hunting activity, the so-called bee-hawking behaviour. These findings are further supported by our linear model analysis, which compared distinct flight abilities between the species (Figure 4; Table 4). According to this model, *V. v. nigrithorax* outperformed *V. crabro* in nearly all evaluated flight and predation-related traits as would be expected from empirical studies (Tan et al., 2007; Sauvard et al., 2018; Cappa et al., 2021; Herrera et al., 2023).

The relative success of these two distinct taxa is likely influenced by key morphological differences as revealed by our findings from multiple perspectives. Our research, has been driven by the aim to better understand how morphological traits alongside behavioural differences previously noted, can help explain their ecological performance. Specifically, we tried to examine how the generalist predator *V. crabro* and the semi-specialized, bee-adapted predator *V. v. nigrithorax* have morphologically adapted to specific predation strategies, such as bee-hawking.

5 Conclusion

Due to its ethological and ecological traits, *V. v. nigrithorax* appears to have gained a competitive edge over the native *V. crabro* in some special areas, i.e. bee-hawking. However, more empirical studies need to be performed to ascertain whether or not *V. v. nigrithorax* can really affect native Vespidae species at the population-level. The invasive *V. v. nigrithorax* behavioural, morphological, and visual adaptations – particularly its efficiency in terms of honeybee predation – have positioned it as a major emerging threat to honeybee populations in western Palaearctic landscapes. These characteristics allow *V. v. nigrithorax* to become

the dominant arthropod predator of honey bees in this region, regardless of the continued presence of its congener *V. crabro*.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

TS: Writing – original draft, Project administration, Funding acquisition, Investigation, Data curation, Supervision, Resources, Conceptualization, Writing – review & editing. BK: Methodology, Writing – original draft, Resources. ÉK-H: Writing – original draft, Resources, Methodology. TD: Writing – original draft, Resources, Investigation, Formal analysis, Data curation. ÁC: Data curation, Validation, Writing – original draft, Software. KK-B: Software, Writing – original draft, Visualization, Validation. AK: Writing – original draft, Methodology, Software, Resources, Visualization, Investigation. SF: Writing – original draft, Writing – review & editing, Data curation, Methodology, Resources, Validation, Software. KS-T: Funding acquisition, Supervision, Resources, Writing – original draft, Data curation. SK: Writing – review & editing, Conceptualization, Investigation, Supervision, Data curation, Methodology, Visualization, Funding acquisition, Writing – original draft, Project administration, Formal analysis.

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Conflict of interest

Authors TD and ÁC were employed by Medicopus Nonprofit Ltd. The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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References

- Araújo, E. D., Costa, M., Chaud-Netto, J., and Fowler, H. G. (2004). Body size and flight distance in stingless bees (Hymenoptera: Meliponini): inference of flight range and possible ecological implications. *Braz. J. Biol.* 64, 563–568. doi: 10.1590/S1519-69842004000400003
- Barbet-Massin, M., Salles, J. M., and Courchamp, F. (2020). The economic cost of control of the invasive yellow-legged Asian hornet. *NeoBiota* 55, 11–25. doi: 10.3897/neobiota.55.38550
- Bass, A., Needham, K., and Bennett, A. M. (2022). First record of *Vespa crabro* Linnaeus (Hymenoptera: Vespidae) in western North America with a review of recorded species of *Vespa* Linnaeus in Canada. *Zootaxa* 5154, 305–318. doi: 10.11646/zootaxa.5154.3.4
- Beggs, J. R., Brockerhoff, E. G., Corley, J. C., Kenis, M., Masciocchi, M., Muller, F., et al. (2011). Ecological effects and management of invasive alien Vespidae. *BioControl* 56, 505–526. doi: 10.1007/s10526-011-9389-z
- Bequaert, J. (1932). A tentative synopsis of the hornets and yellow-jackets (Vespinae; Hymenoptera) of America. *Entomol. Am.* 12, 71–138. doi: 10.5281/zenodo.16436501
- Biehl, L., and Landgrebe, D. (2002). MultiSpec—a tool for multispectral-hyperspectral image data analysis. *Comput. Geosci* 28, 1153–1159. doi: 10.1016/S0098-3004(02)00033-X
- Brodie, E. D. III, and Brodie, E. (1999). Predator-prey arms races: asymmetrical selection on predators and prey may be reduced when prey are dangerous. *Bioscience* 49, 557–568. doi: 10.2307/1313476
- Burnett, N. P., and Combes, S. A. (2023). Close encounters of three kinds: impacts of leg, wing and body collisions on flight performance in carpenter bees. *J. Exp. Biol.* 226, jeb245334. doi: 10.1242/jeb.245334
- Byrne, D. N., Buchmann, S. L., and Spangler, H. G. (1988). Relationship between wing loading, wingbeat frequency and body mass in homopterous insects. *J. Exp. Biol.* 135, 9–23. doi: 10.1242/jeb.135.1.9
- Cappa, F., Cini, A., Bortolotti, L., Poidatz, J., and Cervo, R. (2021). Hornets and honey bees: a coevolutionary arms race between ancient adaptations and new invasive threats. *Insects* 12, 1037. doi: 10.3390/insects12111037
- Carisio, L., Cerri, J., Liroy, S., Bianchi, E., Bertolino, S., and Porporato, M. (2022). Impacts of the invasive hornet *Vespa velutina* on native wasp species: a first effort to understand population-level effects in an invaded area of Europe. *J. Insect Conserv.* 26, 663–671. doi: 10.1007/s10841-022-00405-3
- Choi, M. B., Martin, S. J., and Lee, J. W. (2012). Distribution, spread, and impact of the invasive hornet *Vespa velutina* in South Korea. *Jl Asia-Pac Entomol* 15, 473–477. doi: 10.1016/j.aspen.2011.11.004
- Cini, A., Cappa, F., Petrocchi, I., Pepicello, I., Bortolotti, L., and Cervo, R. (2018). Competition between the native and the introduced hornets *Vespa crabro* and *Vespa*

- velutina*: a comparison of potentially relevant life-history traits. *Ecol. Entomol* 43, 351–362. doi: 10.1111/een.12507
- Danforth, B. N. (1989). The evolution of hymenopteran wings: the importance of size. *J. Zool* 218, 247–276. doi: 10.1111/j.1469-7998.1989.tb02536.x
- Diéguez-Antón, A., Escuredo, O., Seijo, M. C., and Rodríguez-Flores, M. S. (2025). Long-term *Vespa velutina nigrithorax* pressure: honey bee risk survival to alien invasion. *Apidologie* 56, 1–16. doi: 10.1007/s13592-025-01158-z
- Do, Y., Park, W. B., Park, J. K., Kim, C. J., and Choi, M. B. (2022). Genetic and morphological variation of *Vespa velutina nigrithorax* which is an invasive species in a mountainous area. *Sci. Rep.* 12, 4737. doi: 10.1038/s41598-022-08756-2
- Dudley, R. (2002). *The biomechanics of insect flight: form, function, evolution* (Princeton, NJ: Princeton University Press).
- Endler, J. A. (1988). Frequency-dependent predation, crypsis and aposematic coloration. *Philos. T R Soc. Lon. B Biol. Sci.* 319, 505–523. doi: 10.1098/rstb.1988.0062
- Herrera, C., Williams, M., Encarnação, J., Roura-Pascual, N., Faulhaber, B., Jurado-Rivera, J. A., et al. (2023). Automated detection of the yellow-legged hornet (*Vespa velutina*) using an optical sensor with machine learning. *Pest Manag Sci.* 79, 1225–1233. doi: 10.1002/ps.7296
- Hoebcke, E. R., Bartlett, L. J., Evans, M., Freeman, B. E., and Wares, J. P. (2024). First records of *Vespa velutina* (Lepeletier) (color form *Nigrithorax*) (hymenoptera: Vespidae) in North America, an invasive pest of domesticated honeybees. *Proc. Ent Soc. Wash* 126, 193–205. doi: 10.4289/0013-8797.126.2.193
- Jonsson, T. (2023). Micro-CT and deep learning: modern techniques and applications in insect morphology and neuroscience. *Fronts Insect Sci.* 3. doi: 10.3389/finsc.2023.1016277
- Joron, M. (2009). “Aposematic coloration,” in *Encycl Insects* (Cambridge, MA: Academic Press), 33–38. doi: 10.1016/B978-0-12-374144-8.00010-2
- Keszthelyi, S., Orsi-Gibicsár, S., Pal-Fam, F., Somfalvi-Tóth, K., and Balog, A. (2024). Colour polymorphism of cotton bollworm larvae as a function of the type of host plant providing its development. *Front. Ecol. Evol.* 12. doi: 10.3389/fevo.2024.1376435
- Kovac, H., and Stabenheimer, A. (2012). Does size matter? Thermoregulation of ‘heavyweight’ and ‘lightweight’ wasps (*Vespa crabro* and *Vespula* sp.). *Biol. Open* 1, 848–856. doi: 10.1242/bio.20121156
- Kwon, O., and Choi, M. B. (2020). Interspecific hierarchies from aggressiveness and body size among the invasive alien hornet, *Vespa velutina nigrithorax*, and five native hornets in South Korea. *PLoS One* 15, e0226934. doi: 10.1371/journal.pone.0226934
- Landolt, P. J., Sierra, J. M., Unruh, T. R., and Zack, R. S. (2010). A new species of *Vespula*, and first record of *Vespa crabro* L. (Hymenoptera: Vespidae) from Guatemala, Central America. *Zootaxa* 2629, 61–68. doi: 10.11646/zootaxa.2629.1.4
- Laurino, D., Lioy, S., Carisio, L., Manino, A., and Porporato, M. (2019). *Vespa velutina*: An alien driver of honey bee colony losses. *Diversity* 12, 5. doi: 10.3390/d12010005
- Lioy, S., Carisio, L., Manino, A., and Porporato, M. (2023). Climatic niche differentiation between the invasive hornet *Vespa velutina nigrithorax* and two native hornets in Europe, *Vespa crabro* and *Vespa orientalis*. *Diversity* 15, 495. doi: 10.3390/d15040495
- Marden, J. H. (1987). Maximum lift production during takeoff in flying animals. *J. Exp. Biol.* 130, 235–258. doi: 10.1242/jeb.130.1.235
- Mattila, H. R., Otis, G. W., Billen, J., Nguyen, L. T., and Shimano, S. (2022). Comparison of the external morphology of the sternal glands for hornets in the genus *Vespa*. *Biology* 11, 245. doi: 10.3390/biology11020245
- Methven, K., Jeffords, M., Weinzierl, R., and McGiffen, K. (1995). *How to collect and preserve insects* (Illinois Natural History Special Publication no. 17) Champaign, IL, Illinois Natural History Survey.
- Monceau, K., Bonnard, O., and Thiéry, D. (2014). *Vespa velutina*: a new invasive predator of honeybees in Europe. *J. Pest Sci.* 87, 1–16. doi: 10.1007/s10340-013-0537-3
- Monceau, K., Maher, N., Bonnard, O., and Thiéry, D. (2015). Evaluation of competition between a native and an invasive hornet species: do seasonal phenologies overlap? *B Entomol Res.* 105, 462–469. doi: 10.1017/S0007485315000280
- Moraes, S. S., Söderholm, M. S., Aguiar, T. M., Freitas, A. V., and Sihvonen, P. (2023). Micro-CT imaging in species description: exploring beyond sclerotized structures in lichen moths (Lepidoptera: Erebiidae, Arctiinae, Lithosiini). *PeerJ* 11, e15505. doi: 10.7717/peerj.15505
- Onofre, N., Portugal e Castro, M. I., Nave, A., Cadima, I. S. P., Ferreira, M., and Godinho, J. (2023). On the evidence of the European Bee-Eater (*Merops apiaster*) as a predator of the yellow-legged hornet (*Vespa velutina*) and its possible contribution as a biocontrol agent. *Animals* 13, 1906. doi: 10.3390/ani13121906
- Otis, G. W., Taylor, B. A., and Mattila, H. R. (2023). Invasion potential of hornets (Hymenoptera: Vespidae: *Vespa* spp.). *Front. Ins Sci.* 3. doi: 10.3389/finsc.2023.1145158
- Park, W. B., Do, Y., and Choi, M. B. (2024). Ecological integration of *Vespa velutina* Lepeletier 1836 in South Korea: a comprehensive study of co-occurrence and interaction patterns with native social wasps. *Pest Manag Sci.* 80, 6201–6210. doi: 10.1002/ps.8348
- Perrard, A., Arca, M., Rome, Q., Muller, F., Tan, J., Bista, S., et al. (2014). Geographic variation of melanisation patterns in a hornet species: genetic differences, climatic pressures or aposematic constraints? *PLoS One* 9, e94162. doi: 10.1371/journal.pone.0094162
- Perrard, A., Carpenter, J., Kojima, J. I., and Villemant, C. (2013). Phylogeny of hornets: a total evidence approach (Hymenoptera, Vespidae, Vespinae, *Vespa*). *J. Hymenopt Res.* 32, 1–15. doi: 10.3897/jhr.32.4685
- Perrard, A., Lopez-Osorio, F., and Carpenter, J. M. (2016). Phylogeny, landmark analysis and the use of wing venation to study the evolution of social wasps (Hymenoptera: Vespidae: Vespinae). *Cladistics* 32, 406–425. doi: 10.1111/cla.12138
- Robinet, C., Suppo, C., and Darrouzet, E. (2017). Rapid spread of the invasive yellow-legged hornet in France: the role of human-mediated dispersal and the effects of control measures. *J. Appl. Ecol.* 54, 205–215. doi: 10.1111/1365-2664.12724
- Rome, Q., Perrard, A., Muller, F., Fontaine, C., Quilès, A., Zuccon, D., et al. (2021). Not just honeybees: predatory habits of *Vespa velutina* (Hymenoptera: Vespidae) in France. *Ann. Soc. Entomol Fr* 57, 1–11. doi: 10.1080/00379721.2020.1867005
- San Ha, N., Truong, Q. T., Goo, N. S., and Park, H. C. (2013). Relationship between wingbeat frequency and resonant frequency of the wing in insects. *Bioinspir Biomim* 8, 46008. doi: 10.1088/1748-3182/8/4/046008
- Sauvard, D., Imbault, V., and Darrouzet, É. (2018). Flight capacities of yellow-legged hornet (*Vespa Velutina Nigrithorax*, Hymenoptera: Vespidae) workers from an invasive population in Europe. *PLoS One* 13, e0198597. doi: 10.1371/journal.pone.0198597
- Shaw, F. R., and Weidhaas, J. Jr. (1956). Distribution and habits of the giant hornet in North America. *J. Econ Entomol* 49, 275–275. doi: 10.1093/jee/49.2.275
- Smith-Pardo, A. H., Carpenter, J. M., and Kimsey, L. (2020). The diversity of hornets in the genus *Vespa* (Hymenoptera: Vespidae; Vespinae), their importance and interceptions in the United States. *Insect Syst. Diver* 4, 2. doi: 10.1093/isd/ixaa006
- Snyder, W. E., and Evans, E. W. (2006). Ecological effects of invasive arthropod generalist predators. *Annu. Rev. Ecol. Syst.* 37, 95–122. doi: 10.1146/annurev.ecolsys.37.091305.110107
- Tan, K., Radloff, S. E., Li, J. J., Hepburn, H. R., Yang, M. X., Zhang, L. J., et al. (2007). Bee-hawking by the wasp, *Vespa velutina*, on the honeybees *Apis cerana* and *A. mellifera*. *Naturwissenschaften* 94, 469–472. doi: 10.1007/s00114-006-0210-2
- Taylor, B. A., Tembrock, L. R., Sankovitz, M., Wilson, T. M., Looney, C., Takahashi, J., et al. (2024). Population genomics of the invasive Northern Giant Hornet *Vespa mandarinia* in North America and across its native range. *Sci. Rep.* 14, 10803. doi: 10.1038/s41598-024-61534-0
- Team, R. D. C. (2010). *R: a language and environment for statistical computing* (Austria: Vienna). Available online at: <https://www.R-project.org/> (Accessed January 21, 2025).
- Toulkeridou, E., Gutierrez, C. E., Baum, D., Doya, K., and Economo, E. P. (2023). Automated segmentation of insect anatomy from micro-CT images using deep learning. *Nat. Sci.* 3, e20230010. doi: 10.1002/ntls.20230010
- Wei, T., and Simko, V. (2017). *R package “corrplot”: visualization of a correlation matrix (version 0.84)*. Available online at: <https://github.com/taiyun/corrplot> (Accessed January 21, 2025).
- Wickham, H. (2016). “Toolbox,” in *ggplot2: elegant graphics for data analysis* (Springer International Publishing, Cham), 33–74. doi: 10.1007/978-3-319-24277-4_3