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# Sex specificity of dispersal behaviour and flight morphology varies among tree hollow beetle species

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## Abstract

**Background:** Flight performance and dispersal behaviour can differ between sexes, resulting in sex-biased dispersal. The primary sex ratio of populations may also explain dispersal bias between sexes, as this bias may evolve with the primary sex ratio to reduce intrasexual competition. Although dispersal bias between sexes is relevant to population dynamics, there are few studies on sex-biased dispersal in insects. We studied the flight performance and dispersal behaviour of seven saproxylic beetle species associated with tree hollows from a sex perspective. We also analysed the possible coevolution of flight performance with the primary sex ratio.

**Methods:** Wing loading and wing aspect ratio were used as measures of the flight performance of species and sexes. Dispersal behaviour was explored by analysing the frequency of each sex in interception traps *versus* the primary sex ratio obtained by tree hollow emergence traps using contingency tables and posthoc standardized residuals. A more active flight behaviour was expected for the sex with higher capture frequency in the interception traps. To explore the causes of flight performance bias between sexes, we searched for possible correlations between wing loading or wing aspect ratio and primary sex ratio using Pearson's correlation coefficient.

**Results:** Wing loading and wing aspect ratio differed between species and sexes, with flight performance being higher in males than in females for four of the seven species analysed. Dispersal behaviour and flight performance matched in the case of *Elater ferrugineus*; males showed higher flight performance and were the most collected sex in the interception traps (more active flyers). In contrast, the higher flight activity of *Cetonia carthami aurataeformis* females was not correlated with a higher flight performance than that of males. Moreover, we found that a bias in the primary sex ratio towards females is often correlated with a decrease in female flight performance.

**Conclusions:** We stress that flight performance and dispersal behaviour of sexes do not always go hand in hand. Moreover, the relationship between the sex ratio and flight performance bias between sexes is not driven by competition within the most abundant sex. The inclusion of a sex perspective in insect dispersal studies would be useful to detect dispersal bias between sexes and its causes and would allow for further analysis of its effects on population dynamics.

**Keywords:** Saproxylic beetles, Sex biased dispersal, Primary sex ratio, Flight performance, Dispersal behaviour, Wing loading, Wing aspect ratio

## Background

Approaching insect dispersal studies from a sex perspective is informative since the insect dispersal patterns often exhibit large differences at the sex level, affecting

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population dynamics [1, 2]. Studies on dispersal bias between sexes are common in mammals and birds; however, dispersal ability and dispersal behaviour remain underexplored in insects, and few studies have been approached from a sex perspective [3–5].

Species dispersal traits may differ between females and males due to morphological, physiological and behavioural differences [6, 7]. Therefore, when individuals of one sex disperse more than another, sex-biased dispersal (SBD) occurs [7]. Different theoretical hypotheses have been proposed to explain SBD behaviour: the “resource competition hypothesis” (LRC) [8], “local mate competition hypothesis” (LMC) [9] and the “inbreeding avoidance hypothesis” (IAH) [10]. However, the most widely accepted hypothesis to explain SBD is the LRC, which explains why the interaction between competition for local resources and competition for local mates drives population SBD [7, 8]. A higher dispersal rate may evolve in the most abundant sex to reduce intrasexual competition in the natal patch [5, 8, 11, 12]. Selective pressures may therefore act differently on the sexes [2], leading to sexual dimorphism in dispersal behaviour [7, 8, 13–15].

Understanding dispersal bias between sexes in insects and what factors may affect them can help to predict the vulnerability of communities, as dispersal bias has an effect on population dynamics and species’ response to environmental changes [3, 7]. Males can contribute to the genetic rescue of populations, but cannot contribute to demographic rescue as females do [12]. Therefore, populations with male-biased dispersal may be at greater risk of extinction than those with a female bias [12].

One of the most interesting communities for studying insect dispersal behaviour within forest ecosystems are the saproxylic assemblages that inhabit tree hollows.<sup>1</sup> First, tree hollows are considered a keystone microhabitat for European forest biodiversity conservation [16–18]. Second, cavity availability and spatial connectivity are currently jeopardized by several factors, such as forest fragmentation, climatic change, forestry and the abandonment of cultural practices such as tree pollarding (note that tree pollarding accelerates the formation of tree cavities) [16, 19, 20]. Third, fauna that inhabit stable habitats, such as tree hollow microhabitats, are likely to have a lower dispersal capacity than those that inhabit other more unstable habitats [1, 21, 22]. Finally, they include endangered species that are obligate cavity inhabitants [23]. Thus, in the current context of global insect decline [24], it is of particular interest to study the forces that explain the dispersal of such vulnerable assemblages.

Dispersal studies can be approached by direct measurements in the field as a mark–release–recapture method; however, this method presents serious difficulties for investigating individuals who travel long distances [25] and for species whose field observations are hard to evaluate; this is especially true for rare, saproxylic species, whose small population sizes or peculiar habitat (i.e., species that develop in microhabitats such as tree hollows) make them difficult to detect in the field [26, 27]. In these cases, indirect measurements based on flight morphology, such as wing loading (WL) (body mass divided by wing area) and wing aspect ratio (AR) (wing length divided by wing width), can be used as a measure of species flight performance that can help detect possible differences in the success that species, or sexes, might have in colonizing new habitats. Although flight morphology has been questioned as a good indicator of species dispersal [28, 29], several studies have shown that traits such as WL could explain flight performance and a higher propensity to disperse, which indicates that flight morphology and flight performance would be correlated [1, 22, 30–32].

We assessed flight morphology traits and their possible coevolution with primary sex ratio of 7 beetle species associated with tree hollows in Mediterranean *Quercus* forests using different trapping methods (emergence *versus* interception traps) to determine the primary sex ratio and species dispersal behaviour [33]. Morphological dispersal traits such as WL and AR allowed us to analyse potential differences in flight performance between species and sexes. Moreover, we used the primary sex ratio, morphological traits (WL and AR) and the frequency of capture of each sex in the interception traps *versus* the primary sex ratio to analyse the possible causes of SBD and test for possible coevolution of SBD and the primary sex ratio.

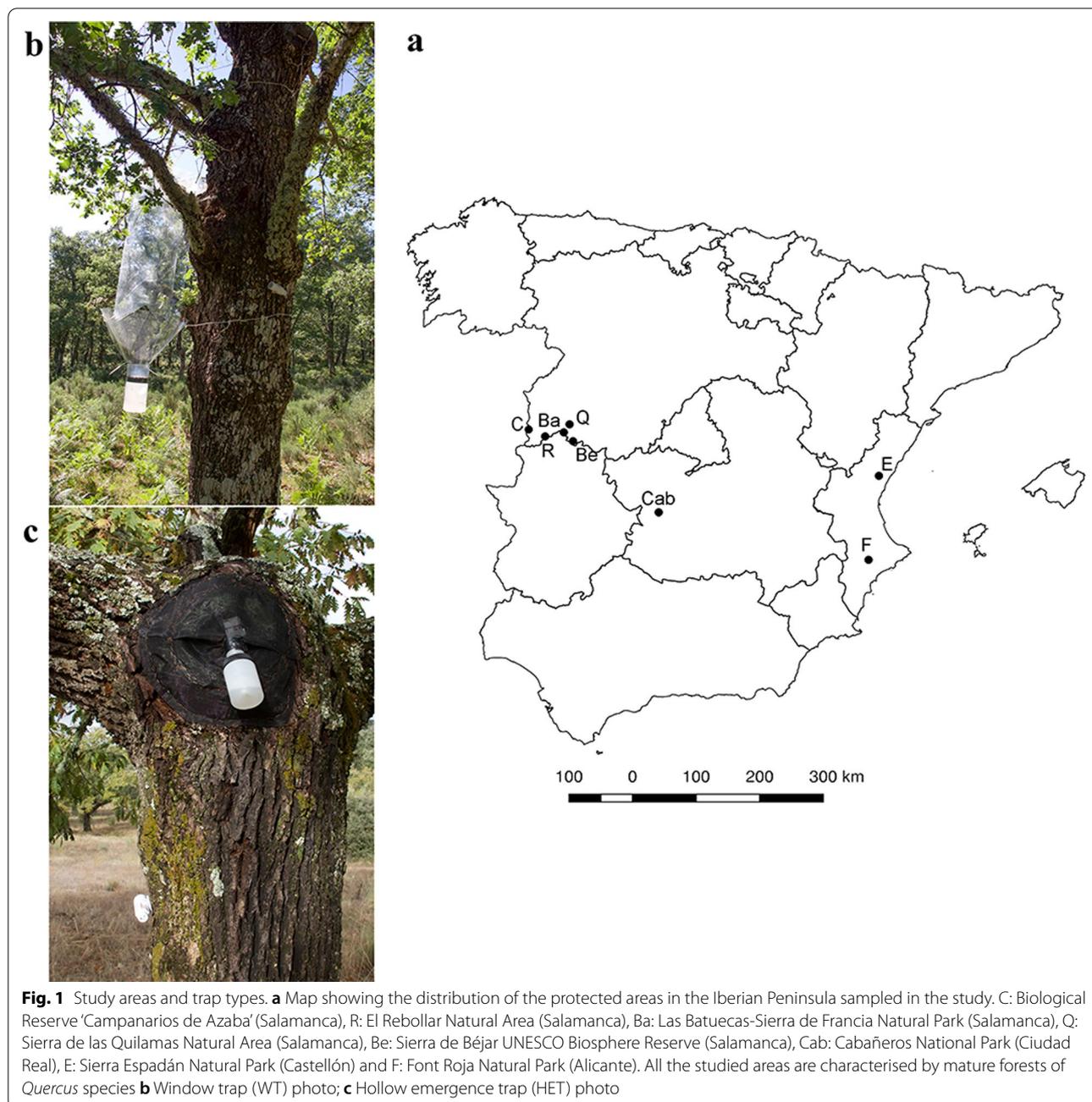
We expected to find differences in flight performance between species and sexes, but these differences are not necessarily related to intraspecific competition [5, 33]. Furthermore, flight performance and dispersal behaviour of species and sexes do not necessarily go hand in hand, as when the benefits of dispersal overcome the physiological costs, dispersal of individuals will increase [12]. Finally, finding of differences in flight performance between sexes, would show the need to include a sex perspective in insect dispersal studies.

## Methods

### Study area

The data used in this study were collected from Mediterranean forests located in 8 protected areas of the Iberian Peninsula: the biological Reserve ‘Campanarios de Azaba’ (Salamanca), Sierra de las Quilamas

<sup>1</sup> Trunk and mould cavities are the main saproxylic microhabitat in veteran trees [16]



Natural Area (Salamanca), El Rebollar Natural Area (Salamanca), Las Batuecas-Sierra de Francia Natural Park (Salamanca), Sierra de Béjar UNESCO Biosphere Reserve (Salamanca), Cabañeros National Park (Ciudad Real), Sierra Espadán Natural Park (Castellón) and Font Roja Natural Park (Alicante) (Fig. 1a, Table 1). All the study areas were characterized by mature forests of *Quercus* species.

#### Beetle sampling and species selection

Beetles were sampled using 228 window traps (WTs) and 272 hollow emergence traps (HETs) (Fig. 1b, c, Table 1) which were placed in the tree species listed in Table 1. Large trees, with a diameter at breast height (DBH) greater than 20 cm, were selected for trap installation. Both trap types were present at all sites and were active for a complete year at each site (Table 1). Each WT

**Table 1** Number of traps and dominant tree species in each studied area

Site	Tree species sampled	Number HET	Number WT	Coordinates	Sampling year
Campanarios	<i>Quercus rotundifolia</i> Lam.	18	15	40° 29.769 N 6° 47.551 W	2010–2011
	<i>Quercus pyrenaica</i> Willd.	10	12		
	<i>Quercus faginea</i> Lam.	3	2		
	<i>Quercus suber</i> L.	0	1		
Quilamas	<i>Q. pyrenaica</i>	33	38	40° 35.642 N 6° 03.201 W	2012–2013 2014–2015
Rebollar	<i>Q. pyrenaica</i>	18	39	40°21.10 N 6°35.05 W	2014–2015 2017–2018
Cabañeros	<i>Q. suber</i>	9	37	39° 23.47 N 4° 29.14 W	2004–2005 2015–2016
	<i>Q. rotundifolia</i>	32	18		
	<i>Q. pyrenaica</i>	22	14		
	<i>Fraxinus angustifolia</i> Vahl.	27	13		
Batuecas	<i>Q. rotundifolia</i>	30	45	40° 27.291 N 6° 08.088 W	2012–2013
Espadán	<i>Q. suber</i>	9	9	39° 52.00 N 0°17.300	2015–2016
Font Roja	<i>Q. rotundifolia</i>	9	9	38°38.51 N 0° 32.46 W	2015–2016
Béjar	<i>Q. pyrenaica</i>	0	12	40°25.26 N 5°47.160	2017–2018
Total		228	272		

Campanarios (Biological Reserve Campanarios de Azaba), Quilamas (Quilamas Natural Area), Rebollar (The Rebollar Natural Area), Cabañeros (Cabañeros National Park), Batuecas (Las Batuecas-Sierra de Francia Natural Park), Espadán (Sierra Espadán Natural Park), and Béjar (Sierra de Béjar UNESCO Biosphere Reserve)

**Table 2** Species observed frequencies of females and males and sex ratio in different sampling methods

Species	HET			WT		
	♂	♀	Primary sex ratio	♂	♀	Sex ratio
<i>Cetonia carthami aurataeformis</i>	130	234	1.8	6	134	22.2
<i>Protaetia cuprea</i>	12	118	9.8	8	210	26.5
<i>Protaetia mirifica</i>	4	14	3.5	0	6	–
<i>Cerambyx wellensii</i>	37	47	1.3	62	37	0.6
<i>Stictoleptura trisignata</i>	27	18	0.7	8	6	0.8
<i>Elater ferrugineus</i>	39	47	1.2	59	19	0.3
<i>Ischnodes sanguinicollis</i>	17	30	1.8	33	17	0.5

Sex ratio was calculated as females/males

consisted of two convergent transparent sheets (73 cm long and 42 cm wide) lying over a funnel and a collection container with preserving liquid (propylene or ethylene glycol) [34, 35] (Fig. 1b). Traps were hung on tree branches 1.5–2 m above the ground. These traps are effective for collecting saproxylic flying beetles associated with different types of tree microhabitats such as bark, tree hollows, dead branches or dead wood in the surroundings of the tree [36–38]. Each HET consisted of a black acrylic mesh that was completely sealed to the tree hollow through staples and a receptacle with preserving liquid (ethylene or propyleneglycol) attached to the mesh [39, 40] (Fig. 1c). This trap type is an effective method to collect species linked to tree hollows shortly after their emergence from immature stages, whether they are

flightless or flying species [35]. Thus, we considered that HETs provide accurate information about populations' primary sex ratio (calculated as females/males) (Table 2) [33]. In contrast, a high abundance of captures of one sex with respect to the other in the interception traps may provide information on the dispersal behaviour of each sex.

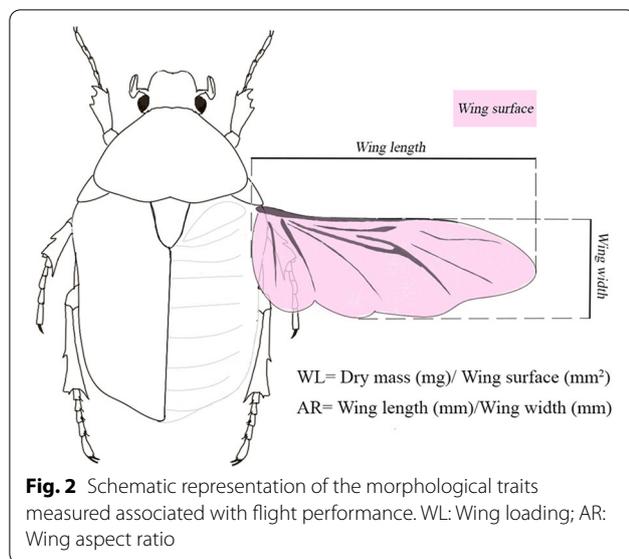
Field studies were carried out from 2004 to 2018, and the samples were collected once a month during one complete year at each sampling site (Table 1).

We selected 7 saproxylic species belonging to 3 beetle families (Coleoptera: Cetoniidae, Elateridae and Cerambycidae) based on their presence in tree hollows, their IUCN Red List category of threat and their functional relevance [41]. All the species selected were represented by

**Table 3** Information about the distribution, biology and Red List category of threat of the species surveyed

Species	Distribution	Biology remarks	IUCN Red List category
<i>Cetonia carthami aurataeformis</i> Curti 1913 (Scarabaeidae: Cetoniidae)	Endemic subspecies of the Iberian Peninsula [42]	Larvae feed on wood and litter in tree hollows [43], while adults are flowers and fruits visitors [44]. This species has been considered an obligate species of tree hollows [33] and an ecosystem engineer <sup>a</sup> of these peculiar microhabitats in Mediterranean forests [46]	–
<i>Protaetia (Potosia) cuprea</i> (Fabricius, 1775) (Cetoniidae)	Palaearctic species [44]	Larvae have been considered facultative inhabitants of tree hollows while adults are flowers and fruits visitors [33, 44]	–
<i>Protaetia (Eupotosia) mirifica</i> (Mulsant, 1842) (Cetoniidae)	Rare species with Mediterranean distribution [47]	Larvae are obligate inhabitants of tree hollows [33]. Adults are often attracted by sugary resources	Vulnerable [23, 48, 49]
<i>Elater ferrugineus</i> Linnaeus, 1758 (Elateridae)	Western Palaearctic species [50]	Larvae and adults are obligate inhabitants of tree hollows. Adults are predators of other saproxylic insects, and larvae can additionally feed on wood mould in cavities [51, 52]. This species has been considered a good indicator of tree hollows beetle diversity [53]	Near threatened [23]
<i>Ischnodes sanguinicollis</i> (Panzer, 1793) (Elateridae)	Palaearctic species [50]	This species is an obligate inhabitant of tree hollows. Larvae and adults are predators [39, 54]	Vulnerable [23]
<i>Cerambyx welsensii</i> (Kuster, 1846) (Cerambycidae)	Palaearctic species [55]	They are considered ecosystem engineers <sup>a</sup> [45, 56]. The larvae are strictly xylophagous, while adults feed mainly on tree exudates or do not feed [57]	Near threatened [23, 49]
<i>Stictoleptura trisignata</i> (Fairmaire, 1852) (Cerambycidae)	Endemic species of the Iberian Peninsula [58]	The larvae of this species are considered xylophagous in different species of <i>Quercus</i> [58], while adults are flower visitors [59]	Near threatened [60]

<sup>a</sup> Are species that provide resources for other species because their activity alters the microhabitat conditions favouring other species fitness [45]



at least 20 individuals to allow for statistical comparisons. The selected species distribution, biology and IUCN Red List category are summarized in Table 3.

The sexes of each species were distinguished by differences in external morphological characters or by analysing the external genitalia when needed.

### Flight morphology

The flight performance of the selected species and their sexes was inferred by indirect measurements of flight morphology, WL and AR [1, 22, 30]. Individuals were dried for 72 h at 30 °C in a drying oven and weighed on an AS82/220.R2 precision scale (RADWAG, Poland) with  $\pm 0.01$  mg accuracy (no individuals weighed less than 1 mg). Samples were rehydrated, and then the left membranous wing was removed and placed with transparent liquid glue on a slide under a cover slip. We measured wing surface, maximum wing length and wing width for 20 individuals (10 females and 10 males) of each species (Fig. 2) using a Leica M205C stereo microscope and Leica Application Suite software version 4.8. WL was calculated by dividing dry mass by wing surface, while AR was calculated by dividing maximum wing length by wing width [22, 61]. A low WL value represents flight that is more energetically efficient and has been interpreted as conferring better flight performance [22, 62]. Conversely, a high AR is indicative of higher wing movement speed [1, 22, 63], which implies that species with the highest AR may be more likely to colonize more habitats and cover longer distances than those with a low AR [64].

### Data analysis

Data from all sampling sites were combined to obtain a sufficient number of individuals for statistical analysis. In our case, all selected sites are located in protected areas characterized by mature forest (with large old trees >20 cm DBH). The intraspecific variability in flight morphology can be affected by landscape structure (i.e., woodlands versus agricultural landscape), forest maturity [29, 33, 65, 66] and food resource availability [67]. Therefore, in this study, no intraspecific differences in flight-related morphology were expected between sites (all included in protected areas), as the landscape structure, forest maturity and conservation are not expected to differ much between sites. To analyse the differences in WL values and ARs between species and sexes, we first tested whether the data were normally distributed with the Shapiro–Wilk normality test [68]. We compared WL values and ARs between species with a Kruskal–Wallis test with multiple comparisons. When significant, we used a posthoc pairwise Wilcoxon test to identify differences between species, and the alpha value was adjusted following Bonferroni correction [69]. Comparisons between both sexes for each species were performed with a nonparametric Mann–Whitney U test for independent samples for WL measurements, except for *P. cuprea* and *P. mirifica*, for which we used a parametric Student's t test. For AR trait comparisons between sexes, we used a parametric Student's t test.

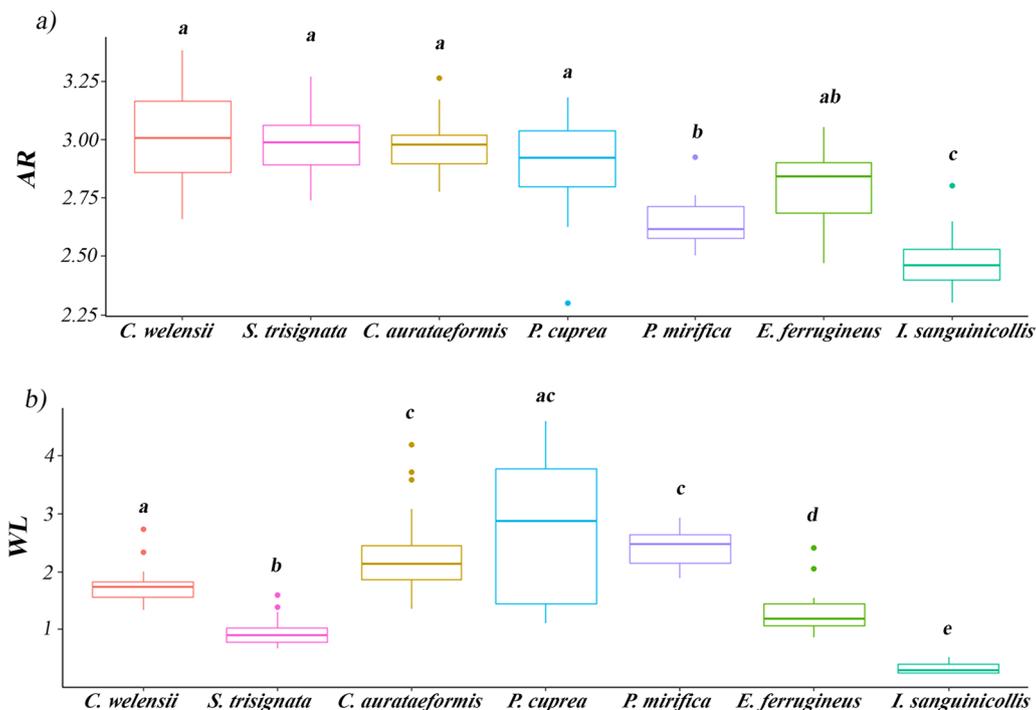
To test the contribution of sex ratio to the species dispersal behaviour, we analysed the frequency of capture of each sex in hollow emergence traps (HETs) with respect to that in interception traps (WTs). For this aim, we used  $2 \times 2$  contingency tables based on a likelihood ratio  $\chi^2$  test [70]. Standardized residuals were analysed to determine whether the observed frequency differed significantly from what would be expected by chance [71, 72].

Moreover, a pairwise correlation was calculated to evaluate the relationships between the primary sex ratio of each species and morphological flight traits by species and sex (female wing loading: WL\_F; male wing loading: WL\_M; female wing aspect ratio: AR\_F; and male wing aspect ratio: AR\_M). For this analysis, we calculated the Pearson rank correlation coefficients and their p values. We considered it as serious collinearity for pairwise correlation where  $\rho \geq 0.75$  [73].

## Results

### Flight morphology of species and sexes

Morphological dispersal traits (WL and AR) showed differences among species (Kruskal–Wallis chi-squared test = 109.6, df = 6, p value < 2.2e-16) (Fig. 3). In general, AR varied less between species than WL.



**Fig. 3** Boxplots showing **a** wing aspect ratio (AR) and **b** wing loading (WL) value for each species. Minimum whiskers, interquartile range boxes (first quartile (Q1), median, third quartile (Q3)), maximum whiskers and outlier symbols are plotted. Bars with different letters mark significant differences in the pairwise Wilcoxon test after Bonferroni correction ( $P < 0.008$ )

*I. sanguinicollis* had the lowest AR, and *P. mirifica* and *E. ferrugineus* also showed a low AR (Fig. 3a). In contrast, WL differed among all species, except for Cetoniidae species (Fig. 3b). *I. sanguinicollis* and *S. trisignata* showed the lowest WL. In contrast, Cetoniidae species showed the highest WL (worst flight efficiency compared with the rest) (Fig. 3b).

Differences in flight performance between sexes were found within some species (Fig. 4). *E. ferrugineus* and *S. trisignata* presented a lower AR in females than in males. Similarly, *S. trisignata*, *P. cuprea* and *I. sanguinicollis* also showed significantly higher WL in females (Fig. 4).

#### Dispersal behaviour

The results showed significant differences in the capture frequency of females and males of *C. c. aurataeformis* and *E. ferrugineus* for each type of trap (Table 4). However, the differences varied among them. Females of *C. c. aurataeformis* were captured more often than expected by chance in the interception traps (WTs) (indicating that the sex was more active in flight) than in the hollow emergence traps (HETs) (reflecting the primary sex ratio). In contrast, males of *E. ferrugineus* were captured more often than expected by chance in WTs (Table 4).

#### Species sex ratio and flight performance bias between sexes

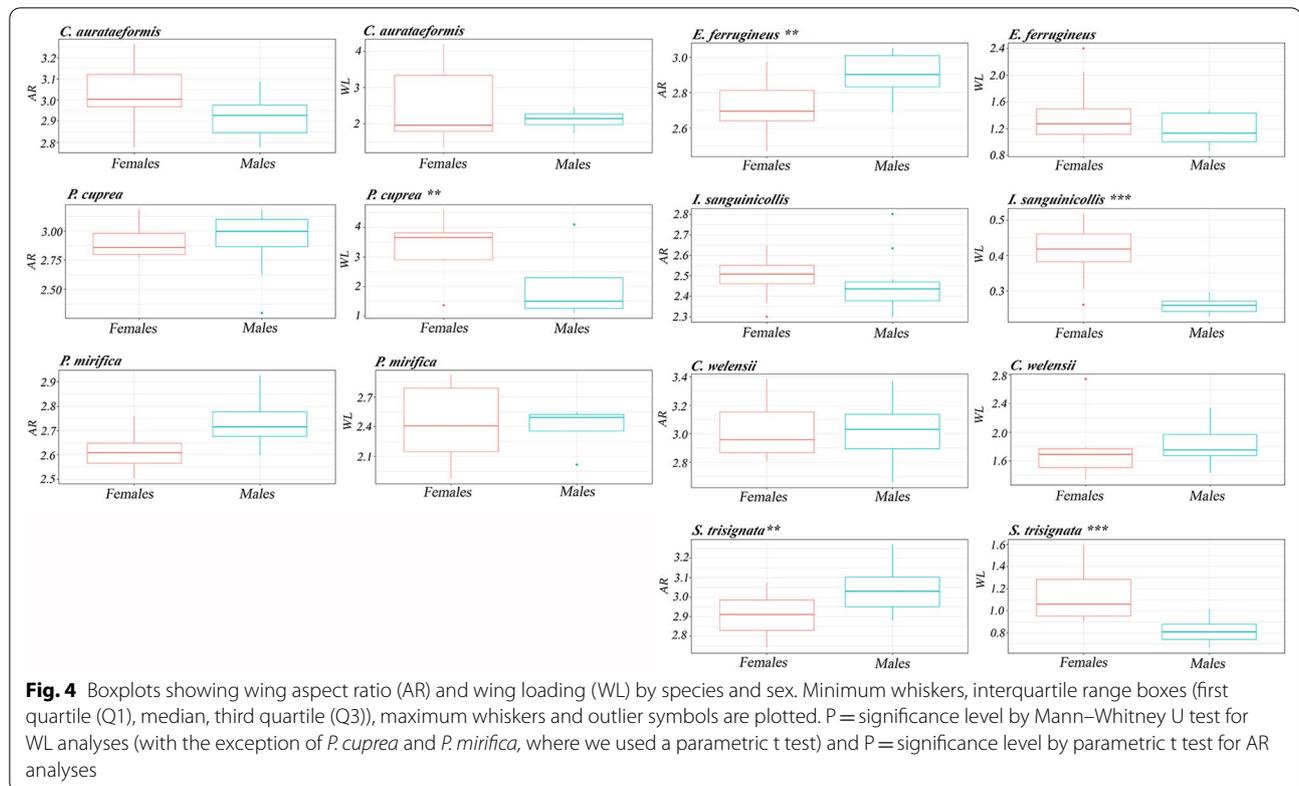
The results of Pearson correlation coefficients showed moderate collinearity between the primary sex ratio and WL<sub>F</sub>, while high collinearity ( $\rho \geq 0.75$ ) was shown between WL<sub>F</sub> and WL<sub>M</sub>. According to our results, an increase in the sex ratio biased towards females seems to be linked with an increase in WL<sub>F</sub> (Fig. 5).

#### Discussion

Our results showed that the inclusion of a sex perspective in insect dispersal studies could help not only to better understand the dispersal behaviour of some saproxylic beetle species inhabiting tree hollows but also to detect flight performance bias between sexes (key to population dynamics) and its possible causes. Additionally, our results suggest that intrasexual competition is not always a consequence of an imbalance in the sex ratio of populations. For the same reason a dispersal bias in favour of the more abundant sex according to the primary sex ratio cannot be assumed.

#### Flight performance and dispersal behaviour

Morphological traits (WL and AR) were used to assess the flight performance of rare species that are poorly

**Table 4** Pearson's  $\chi^2$  significance from the  $2 \times 2$  contingency table test and post hoc standardized residuals

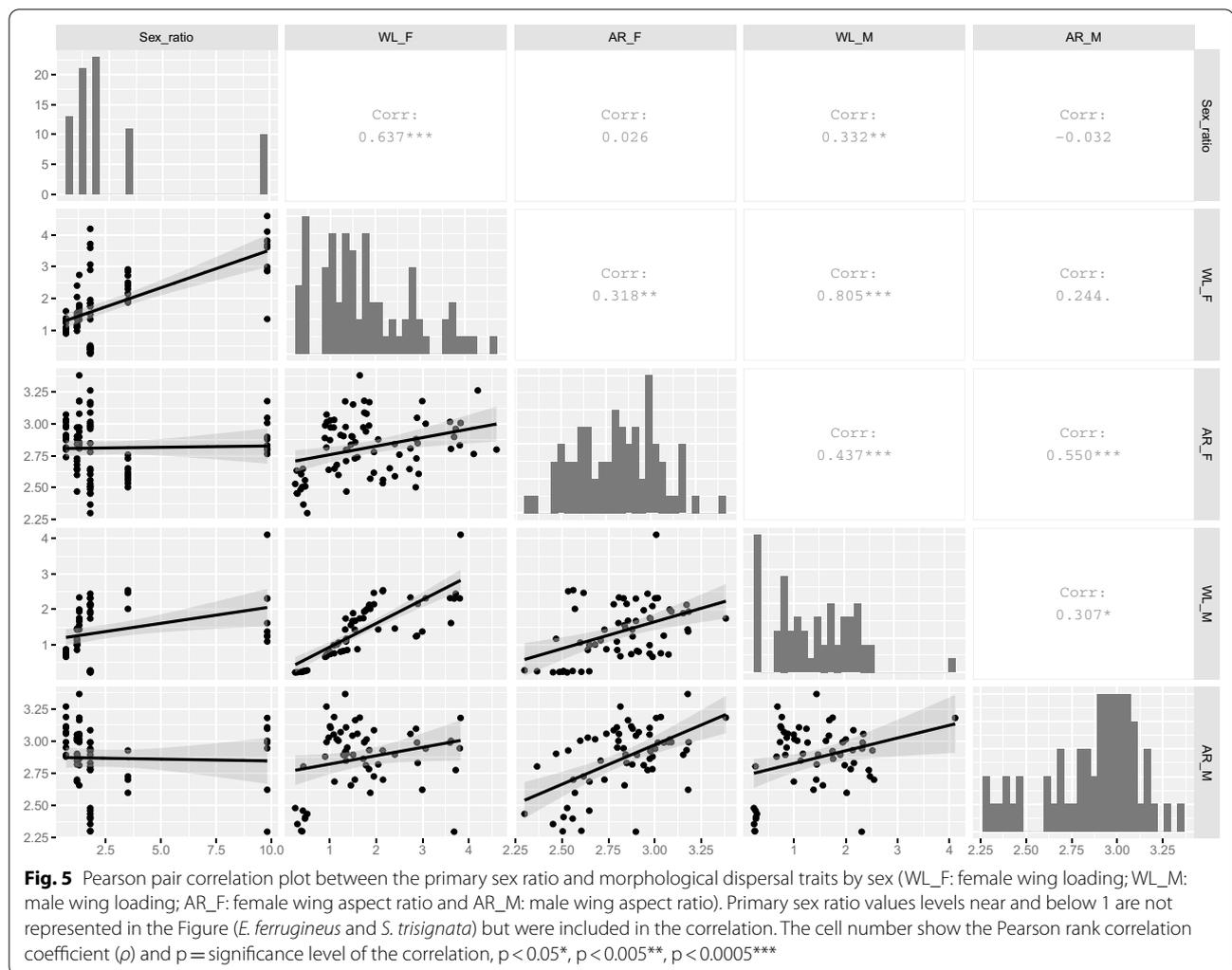
Species	Pearson's $\chi^2$	Df	Prob. level	Standardized residuals post-hoc (Z critical value)		
				Sex	HET	WT
<i>Cetonia carthami aurataeformis</i>	50.05	1	<b>= 0.0000</b>	Females	<b>1.07</b>	<b>2.97</b>
				Males	<b>2.62</b>	<b>- 4.74</b>
<i>Protaetia cuprea</i>	3.67	1	<b>0.0311</b>	Females	- 0.41	0.31
				Males	1.65	- 1.27
<i>Protaetia mirifica</i>	1.6	1	0.5271 <sup>a</sup>	-	-	-
<i>Cerambyx wemensii</i>	5.5905	1	<b>0.01806</b>	Females	1.36	- 1.25
				Males	- 1.25	1.15
<i>Stictoleptura trisignata</i>	4.291e-31	1	1	-	-	-
<i>Elater ferrugineus</i>	14.373	1	<b>0.0001499</b>	Females	<b>2.10</b>	<b>- 2.21</b>
				Males	<b>- 1.72</b>	<b>1.81</b>
<i>Ischnodes sanguinicollis</i>	7.4782	1	<b>0.006245</b>	Females	1.51	- 1.46
				Males	- 1.46	1.42

Significant values in bold

<sup>a</sup> Yate's correction was applied to the  $\chi^2$  test when the expected frequency value was less than 5

detectable with direct measurements in the field. Although the use of WL and AR as a proxy to measure the dispersal of insect species has been questioned [28, 29], the study of flight-related traits has been extensively studied in some insects orders such as Lepidoptera,

Trichoptera or Hemiptera, where the results could explain the higher migratory success of species or sexes [26, 31, 32]. In our results, WL highlighted as the most informative morphological trait for all species, as WL presented higher differences between species and sexes



than AR. A low WL is related to higher energy efficiency to flight and better flight performance [22]. AR shows the flight type of the species, where a high AR shows a higher wing movement speed, which seems to confer the species with a better ability to travel from its natal patches [22, 63, 64]. Accordingly, if both a low WL and a high AR are interpreted as surrogates for increased flight performance, our results show an inconsistency in the case of the Vulnerable *I. sanguinicollis*: this species presented a more energy-efficient flight but a low-speed flight (Fig. 3a, b). However, we believe that this need not be contradictory, as WL and AR measure different traits on flight performance. Therefore, species could have good flight efficiency with respect to body mass but slow flight, characterized by gliding flight according to wing morphology. Based on WL, *I. sanguinicollis* had a higher flight performance than the other species, despite being listed as Vulnerable on the IUCN red list. Hagge et al. [28] also found several good dispersal species among

the European red-listed saproxylic beetles. This could be related to the threat posed, even to good dispersers, by their dependence on widely dispersed resources [28]. In contrast to *I. sanguinicollis*, in the also Vulnerable *P. mirifica*, both characters (WL and AR) move the same way, with a low flapping flight combined with a low efficiency flight—this latter character is shared by the other cetonid species (Fig. 3a, b). We can therefore confirm that *P. mirifica* is a poor disperser, consistent with the relict distribution of this species—with 41 localities with Mediterranean distribution (some of them probably already extinct) [47, 74, 75]. As an obligate saproxylic species, this low flight performance together with the regression of their habitats and microhabitats (tree hollows) [6, 16, 76] could seriously jeopardize their populations in the near future. Similarly, the other cetonid species, such as *C. c. aurataeformis* and *P. cuprea*, may also be threatened by habitat loss and connectivity (related to habitat fragmentation) due to their high WL values (Fig. 3a, b). These

results are of particular importance, as habitat fragmentation often results in increased autocorrelated extinction patterns that change the cost–benefit balance and lead to less successful emigration overall and increased long-distance dispersal [77]. WL and AR revealed differences in flight performance between sexes for some species, such as *E. ferrugineus*, *P. cuprea*, *I. sanguinicollis* and *S. trisignata*; males always had higher flight performance than females (Fig. 4). However, is flight performance a mirror of the dispersal behaviour? The analysis of the differences in the frequency of capture of females and males among traps showed that in *E. ferrugineus*, males would be (1) the sex that travels longer distances and (2) more active in flight than females (Fig. 4), thus having a higher probability of being captured in interception traps (WTs) than in hollow emergence traps (HETs) (Table 4). Accordingly, *E. ferrugineus* dispersal behaviour could be explained by flight performance (the sex with higher flight performance is also the most frequently captured in interception traps). Our results for *E. ferrugineus* are in agreement with the results obtained by Zauli et al. [27], where males were observed to cover greater distances than females. In contrast, the flight performance of *C. c. aurataeformis* did not differ between sexes; thus, the higher capture frequency of females in the WTs was better explained by differences in dispersal behaviour than by the flight performance of females (Fig. 4). Notice that *Cetonia* adults, unlike *E. ferrugineus*, are not saproxylic, and only females search for tree hollows to oviposit. In this way, the postreproductive behaviour of cetonid species, where females lead their dispersal movement towards oviposition sites such as tree hollows and males disperse towards flowers for feed, leaving the breeding sites, reduces the probability of male capture in WTs with respect to females [33, 78]. This supports the theory that females and males may differ in the type of resources they exploit and therefore the impact of resource constraints may vary between the two sexes, limiting their reproductive success, also producing a bias in the behaviour of each sex [79].

### Species sex ratio and sex-biased dispersal

SBD is expected in populations with a high sex ratio bias. Theoretical predictions say that the most abundant sex in natal patches undergoing intense competition would be the most dispersive sex [5, 8, 11, 12, 79]. However, we found a correlation between a female-biased primary sex ratio and low female dispersal ability based on WL (Figs. 4 and 5). This result could be explained by the following: (1) females may have higher dispersal costs than costs due to competition, (2) intrasexual competition is not a decisive factor to induce dispersal bias, or (3) intrasexual competition for oviposition sites or feeding

resources (pollen or run sap) simply does not exist within females [12, 62]. Similarly, we know that competition within the saproxylophagous guild that inhabit tree hollows does not seem to be a decisive factor, at least at the interspecific level [80]. Field studies with mark–release–recapture techniques could provide complementary insights into our findings about species dispersal behaviour [1, 81, 82]. Other factors should also be considered to test these theoretical predictions, as the potential benefits of dispersal could overcome physiological costs [12], which could result in an effective dispersal bias between sexes.

### Conclusions

Our results shed light on the value of including a sex perspective in studies related to insect dispersal. Furthermore, the exploration of the possible causes of SBD is useful to better predict the extinction risk of species, as populations of species with poorly dispersive females are more vulnerable to extinction due to their involvement in population dynamics [13]. Based on our results, we stress that SBD is not necessarily driven by intrasexual competition within the most abundant sex. Accordingly, a coevolution between the sex ratio of populations and bias in sex flight performance in saproxylic insects may not always be assumed.

### Abbreviations

SBD: Sex bias dispersal; LRC: Local resource competition; LMC: Local mate competition; IH: Inbreeding hypothesis; WL: Wing loading; AR: Wing aspect ratio; WT: Window trap; HET: Hollow emergence trap; WL\_F: Females wing loading; WL\_M: Males wing loading; AR\_F: Females wing aspect ratio; AR\_M: Males wing aspect ratio.

### Acknowledgements

We wish to thank J. Jordán-Nuñez for his help with the statistical analyses.

### Author contributions

SMP: conceptualization, methodology, data curation, measurement of functional traits, formal analysis, writing-original draft, reviewing and editing. EG: reviewing, editing and funding acquisition. EM: conceptualization, methodology, data curation, formal analysis, reviewing and editing, funding acquisition. All authors read and approved the final manuscript.

### Funding

Financial support was provided by the ‘Ministerio de Economía, Industria y Competitividad’ (CGL2016-78181-R) and by the Ministerio de Ciencia e Innovación (PID2020-115140RB-I00) granted to EM. This research is part of Sandra Martínez Pérez’s PhD studies granted by ‘Ministerio de Economía, Industria y Competitividad’ (BES-2017-080278).

### Availability of data and materials

The datasets used and/or analysed during the current study are available from the corresponding author.

### Declarations

#### Ethics approval and consent to participate

Not applicable.

**Consent for publication**

Not applicable.

**Competing interests**

The authors declare no competing interest.

Received: 2 June 2022 Accepted: 15 September 2022

Published online: 24 September 2022

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