

Sexual dimorphism in excess power index of four North American native bees (Hymenoptera, Andrenidae, Apidae, and Halictidae)

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Academic editor: Jack Neff | Received 10 December 2022 | Accepted 31 March 2023 | Published 11 April 2023

<https://zoobank.org/CCF95B60-A562-45E1-8B25-2F7233EAE096>

Citation: Vigueira PA, Vigueira CC, Campbell JW, Ladner S, Hayes G, Riser E (2023) Sexual dimorphism in excess power index of four North American native bees (Hymenoptera, Andrenidae, Apidae, and Halictidae). *Journal of Hymenoptera Research* 96: 121–128. <https://doi.org/10.3897/jhr.96.98652>

Abstract

A multitude of hymenopteran species exhibit sexual dimorphism for simple traits, such as color, size, or antennal segment number. These differences can reflect selection for specialized biological roles, many of which have not been documented for the majority of bee and wasp species. The excess power index (EPI) is an estimate of insect flight performance that is inferred by the combination of several morphological characteristics. We compared the female and male EPIs in four species of native bees: *Agapostemon virescens* Fabricius, *Andrena carlini* Cockerell, *Melissodes bimaculata* Lepeletier and *Xylocopa virginica* L.. While females of each species had a significantly larger whole body mass, males had a significantly larger EPI. A larger body mass for females is associated with egg laying abilities and foraging behavior. Male fitness may be dependent on EPI; males that have greater flight capacity can travel further or remain in flight for longer time periods in search of mates.

Keywords

excess power index, flight machinery, sexual dimorphism, wing loading

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Introduction

In North America, it is estimated that there are 4,000 different species of native bees (Michener 2007). Native bees are important pollinators for a multitude of crops (Allen-Perkins et al. 2022) and non-crop plants alike (Ollerton et al. 2011). However, native bees have been in decline due to numerous anthropogenic activities (Cameron et al. 2011; Abbate et al. 2019). Despite their economic and ecological importance, the basic biology and life history of the vast majority of native bee species have remained unstudied. Observational field studies of bees can be challenging, time consuming, and often unsuccessful at finding species of interest. One indirect method of learning about native bee biology is through the use of preserved specimens. Museum specimens have been used to assess population declines of native bees (Colla et al. 2012), pollen sources utilized (Kleijn and Raemakers 2008; Scheper et al. 2014), phylogenetics (Vaudo et al. 2018), and species determination via morphometrics and DNA barcoding (Ndungu et al. 2017).

Previous studies have used flight-relevant morphological features of bees to predict an individual's flight performance potential that is described in a composite value called Excess Power Index (EPI). Excess Power Index has been used to calculate the maximum power that an individual bee has in order to maintain a steady flight at equilibrium in relation to the bee's body proportions and wing dimensions (Hepburn et al. 1998). These measurements have been used to compare flight mechanics of workers from different honey bee subspecies (*Apis mellifera* subsp. L.), honey bee species (*Apis* spp. L.), and castes (Hepburn et al. 1998; Hepburn et al. 1999; Radloff et al. 2003). Additionally, EPI has been used to examine relationships among native and non-native bumble bees (*Bombus* spp. Latreille) (Polidori and Nieves-Aldrey 2015), compare progeny size of *Osmia bicornis* L. (Seidemann 2014) and *Osmia lignaria* Say (Helm et al. 2021) via provision studies, and explore flight morphology and metabolic rates of *Megachile rotundata* Fabricius (Grula et al. 2021). EPI is a composite variable that includes the ratio of mesosomal mass/whole body mass (r) and wing loading (L), which is a ratio of whole body mass/total wing area.

In this study, we calculated EPI for four native bee species from three different families (Andrenidae, Apidae, and Halictidae). Our objectives were to determine if EPI varied among sexes of solitary bees and whether these morphological measurements could be used to predict flight behavior. We hypothesized that EPI would differ between the sexes due to the variable ecological and social roles that male and female bees play.

Materials and methods

Bee collection

Agapostemon virescens Fabricius (N = 20 ♀ and 20 ♂) and *Andrena carlini* Cockerell (N = 12 ♀ and 12 ♂) were collected by Sam Droege at the USGS Patuxent Wildlife Research Center. *Melissodes bimaculata* Lepeletier (N = 72 ♀ and 21 ♂) were captured

near Scooba, Mississippi (Campbell et al. 2016). *Xylocopa virginica* L. (N = 19 ♀ and 18 ♂) were captured in St. Louis, Missouri in May 2015. All bees were either collected with sweep nets or colored pan traps. Additionally, all bees were collected from small locales to limit geographical/environmental differences in body size. These four species were chosen due to their commonness and easily distinguishable features.

Specimen preparation and trait measurements

Whole specimens were dried for 72 hours at 45 °C prior to determination of whole body mass (WBM) and mesosomal mass (MM) via a digital scale. One forewing and one hind wing were removed and flattened between glass microscope slides (Darveau 2005). Each mounted wing was photographed with a 5mm size standard in the frame using a dissecting microscope (Zeiss). Images were assembled using Tps Utility software (Rohlf 2012), and wing area was determined with the TpsDIG software package (Rohlf 2005). We assumed symmetry between the paired wings, and therefore, we calculated total wing area (TWA) by doubling the forewing and hindwing areas that were measured from each specimen: $TWA = (\text{forewing area} * 2) + (\text{hindwing area} * 2)$.

Excess power index calculation and statistical analysis

The excess power index (EPI) was calculated with the following formula:

$$EPI = \sqrt{\frac{(\text{Mesosomal Mass} / \text{Whole Body Mass})^2}{\text{Whole Body Mass} / \text{Total Wing Area}}}$$

We performed pairwise comparisons of single and composite variables between males and females of each species using the Mann-Whitney U test. To better understand the relative contributions of each portion of the EPI formula to differences between sexes, we compared two additional composite variables: 1. the ratio of mesosomal mass/whole body mass (r) and 2. the ratio of whole body mass/total wing area or wing loading (L). We judged statistical significance to be $p < 0.05$.

Results

The whole body mass of females was significantly larger than males in all four bee species (Table 1). For *A. virescens* and *X. virginica*, the r and L values were both significantly different between females and males. Males had both an elevated r and lower L compared to females, both contributing positively to a male-biased dimorphism in EPI (Fig. 1, Table 1). In contrast, both *M. bimaculata* and *A. carlini* r values were not significantly different between male and female cohorts (Table 1). However, male L was significantly lower than females in both species, resulting in a male-biased dimorphism in EPI (Fig. 1, Table 1). Wing surface area was significantly different between sexes in all bee species except *X. virginica*. See Table 2 for all test statistics.

Table 1. Mean morphological measurements (\pm SE) for four male and female native bee species that were used to calculate Excess Power Indices (EPI). An * indicates statistical significance between male and female of each bee species at $P = 0.05$.

Bee Species/Sex	WBM (mg)	MM (mg)	r	WSA (mm ²)	L (mg/mm ²)
<i>Agapostemon virescens</i> ♀, N = 20	15.76 (0.76)*	5.98 (0.28)*	0.38 (0.005)*	50.65 (1.06)*	0.31 (0.009)*
<i>Agapostemon virescens</i> ♂, N = 20	8.25 (0.36)	3.61 (0.17)	0.44 (0.006)	36.20 (0.75)	0.23 (0.007)
<i>Andrena carlini</i> ♀, N = 12	36.64 (3.03)*	11.18 (.64)*	0.31 (0.01)	67.32 (1.60)*	0.54 (0.04)*
<i>Andrena carlini</i> ♂, N = 12	11.02 (0.40)	3.30 (0.30)	0.30 (0.03)	44.66 (1.47)	0.25 (0.007)
<i>Melissodes bimaculata</i> ♀, N = 72	41.40 (0.90)*	14.21 (0.30)*	0.34 (0.003)	87.14 (0.80)*	0.47 (0.008)*
<i>Melissodes bimaculata</i> ♂, N = 21	27.66 (1.37)	9.50 (0.44)	0.35 (0.006)	76.05 (1.53)	0.36 (0.01)
<i>Xylocopa virginica</i> ♀, N = 19	259.17 (14.44)*	68.96 (2.22)	0.27 (0.01)*	188.52 (3.72)	1.36 (0.06)*
<i>Xylocopa virginica</i> ♂, N = 18	152.15 (4.97)	62.29 (3.23)	0.41 (0.02)	196.69 (3.93)	0.77 (0.02)

WBM = whole body mass, MM = mesosomal mass, r = mesosomal/body mass ratio, WSA = wing surface area, L = wing loading.

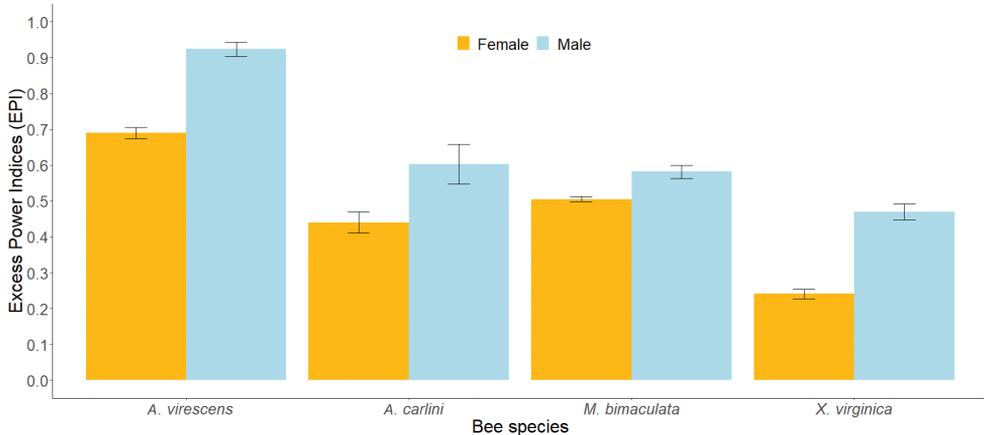


Figure 1. Excess Power Indices (EPI) (\pm SE) of four native bee species (*Agapostemon virescens*, *Andrena carlini*, *Melissodes bimaculata*, *Xylocopa virginica*) and their corresponding sex. All Mann-Whitney U tests found that all males of each species had a significantly higher EPI compared to females at $p < 0.05$.

Discussion

Differences in body size of male and female insects can result in different thermoregulatory and flight abilities (Gilchrist 1990). In general, total wing area in bees has been shown to be positively related to body mass (Bullock 1999) as might be expected. Body mass differences and wing loading in these four bee species were probably due to mating and foraging behaviors. Male bees invest no energy into their offspring; their activities are primarily directed to finding mates. Thus, male bee activity is driven by (1) the need to thermoregulate flight muscles, (2) finding enough nectar to power flight, and (3) find and mate with females (Willmer and Stone 2004). Thus, having a smaller body but increased wing loading should allow males to fly longer distances or remain in flight for longer time periods in search of females but also limit the amount of nectar

Table 2. Mann-Whitney U test statistics for morphological parameters and Excess Power Indices.

	WBM	MM	r	WSA	L	EPI
<i>Andrena carlini</i>	$z = 4.13,$ $P < 0.00001$	$z = 4.13,$ $P < 0.00001$	$z = 0.14,$ $P = 0.89$	$z = 4.13,$ $P < 0.00001$	$z = 4.13,$ $P < 0.00001$	$z = 2.45,$ $P = 0.014$
<i>Melissodes bimaculata</i>	$z = 5.87,$ $P < 0.00001$	$z = 5.93,$ $P < 0.00001$	$z = 0.11,$ $P = 0.91$	$z = 5.22,$ $P < 0.00001$	$z = 5.80,$ $P < 0.00001$	$z = 3.92,$ $P = 0.001$
<i>Agapostemon virescens</i>	$z = 5.26,$ $P < 0.00001$	$z = 4.93,$ $P < 0.00001$	$z = 4.65,$ $P < 0.00001$	$z = 5.37,$ $P < 0.00001$	$z = 4.75,$ $P < 0.00001$	$z = 5.32,$ $P < 0.00001$
<i>Xylocopa virginica</i>	$z = 4.85,$ $P < 0.00001$	$z = 1.84, P =$ 0.066	$z = 4.60,$ $P < 0.00001$	$z = 1.14,$ $P = 0.25$	$z = 5.18,$ $P < 0.00001$	$z = 4.60,$ $P < 0.00001$

needed to sustain themselves. Additionally, many male bee species (e.g., *A. carlini*) will ‘patrol’ flowers in search of females (Schrader and LaBerge 1978). Male bees, including *A. virescens* and *M. bimaculata* will sleep inside flowers (Rau 1938; Abrams and Eickwort 1981). This male-biased dimorphism in EPI, a composite variable that describes the predicted flight capacity of an individual based on mass and morphological attributes, can be used to predict flight behavior between bee sexes.

Female bee activities are primarily driven by the need to collect floral resources (e.g., pollen and nectar) to provision themselves and for their offspring. Unlike social bee species, solitary females complete all nest construction and provisioning on their own. Although some species in this study are considered communal nesters, each individual female only provisions her own nest(s). Solitary bees provision each brood cell sequentially and must provide enough food resources for each one (mass provisioning), which will take multiple foraging trips per brood cell (Danforth et al. 2019). Having a larger body mass may enable females to better thermoregulate body temperature enabling them to forage in less than optimal conditions (Stone 1993). Additionally, a larger body size should also allow for carrying larger loads of pollen and nectar and the ability to fly to farther flower patches (Skandalis et al. 2009). Indeed, larger-bodied female bee species have been correlated with increased foraging ranges (Greenleaf et al. 2007). However, female bees may be faced with an evolutionary tradeoff; larger body sizes can carry more provisions but have reduced flight capacity (Seidelmann 2014). Alternatively, larger body size in female bees has not always shown consistent patterns when relating body size to fecundity (Tepedino et al. 1984) and may contribute to higher parasitism rates by parasitoids (Müller et al. 1996). Thus, multiple evolutionary pressures may contribute to bee body size.

Among the bee species utilized for this study, *X. virginica*, a cavity nesting species, is probably the most thoroughly studied. Males often compete in intrasexual aggression which is mediated primarily through the body size of the males (Barthell and Baird 2004). The interactions between these males are often done in the form of aerial pursuits, which indicates the necessity for the males to have a better EPI in order to fly more efficiently for these male aggression encounters (Barthell and Baird 2004). Interestingly, despite the difference in EPI between male and female *X. virginica*, wing area did not significantly differ. The ecologies of the other three bee species in this study are

poorly documented. However, they are all ground nesters but include a range of nesting habits from communal nesters for *A. virescens* (Eickwort 1981) to solitary nests for *A. carlini* (Schrader and LaBerge 1978). All four bee species feed on a variety of plants for pollen and nectar and, thus, are considered polylectic (Mitchell 1960, 1962).

Conclusion

The four bee species utilized for this study comprised three ground-nesting species (*A. carlini*, *M. bimaculata*, *A. virescens*) and one cavity nesting bee (*X. virginica*). Despite the differences in nesting and the wide taxonomic differences, the morphological measurements between the sexes showed similar trends. Although we only assessed four species, this proof of concept would also be expected for other solitary bees that have similar life histories and ecologies. To our knowledge, this is the first report of EPI measurements on non-*Apis/Bombus* bees other than *O. bicornis*, *O. lignaria*, and *M. rotundata* (Seidelmann 201; Grula et al. 20214; Helm et al. 2021) and the only wild bee species utilized from the Nearctic for this type of study. Utilizing EPI for other wild bee species may allow for inferences to be made regarding male/female behaviors but also comparative studies across landscapes and environmental conditions.

Acknowledgements

We thank Sam Droege of the USGS Patuxent Wildlife Research Center for providing specimens. This work was completed at High Point University.

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