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Habitat Exploration and Foraging in a Dominant Hover Fly (*Melangyna*) is Sex-Dependent

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ABSTRACT

Distinct behaviours between males and females within the same species can promote differences in the use of resources between sexes, which can have profound consequences on ecosystem processes, such as pollination. Despite this, studies on floral visitation often focus on the relationships between floral visitors and plants at the species level, neglecting the intraspecific differences between male and female insect floral visitors. This study investigates intraspecific differences in the use of floral resources by male and female *Melangyna*, a dominant group of hover flies. Our year-long observations reveal distinct behaviours in hovering and foraging between the sexes and among the seasons. We also present evidence of sexual dimorphism, with males being larger than females. These behavioural and physical differences lead to distinct use of floral resources by each sex, which could have significant implications for plant reproduction. Our findings underscore the need to consider intraspecific sexual differences in future studies on floral visitation and pollination.

1 | Introduction

Differing foraging behaviours between males and females of the same species have been observed in some pollinator taxa, for example, in bees (Roswell et al. 2019) and butterflies (Ehl et al. 2018). These differences in foraging behaviour are often associated with differing nutritional requirements and may decrease the amount of shared resources and intraspecific competition (Roswell et al. 2019; Ehl et al. 2018). Beyond this, sexual selection and intraspecific niche divergence hypotheses suggest that differences in resource use between sexes result in sexual dimorphism (Temeles et al. 2010; Shine 1989; Pearson et al. 2002). Understanding differences in resource use between sexes provides insights into the biology and foraging behaviours of pollinator taxa, like hover flies.

Hover flies are an important group of pollinators with an almost global distribution (Dunn et al. 2020). Additionally, the larvae of numerous hover fly species are predators of hemipterans associated with food crops (Dunn et al. 2020), thus understanding the patterns in insect–plant interactions of this charismatic group of insects is relevant not only for their intrinsic value but also from a food production perspective. Male and female hover flies have similar energetic needs met by nectar intake, but females have additional metabolic requirements related to gestation and oviposition (Soleyman-Nezhadiyan 1996) and need to supplement their carbohydrate intake with a source of food that provides them with amino acids, such as pollen (Irvin et al. 1999). Understanding differences in resource use between sexes in hover flies provides insights into the biology of this important group of pollinators. This study aims to observe differences in resource use between male

and female hover flies (*Melangyna*) in Sydney, Australia; and to explore if sexual dimorphism exists in *Melangyna*. We hypothesised that (1) when hovering, *Melangyna* show less difference in the identity of the plants hovered above between sexes, because they are in an exploratory phase; (2) when visiting flowers, *Melangyna* show more difference in resource use between sexes, because males and females have different dietary needs that drive their floral preferences and (3) males are larger than females.

2 | Methodology

2.1 | Melangyna–Plant Interaction Surveys

We conducted surveys of *Melangyna* at 30 sites across Sydney, each visited once per season from Winter 2019 to Spring 2020. We randomly selected public urban greenspaces between 0.5 and 118 ha in the metropolitan area of Sydney. A 100-m transect was used for visual surveys of *Melangyna*. Surveys were conducted between 9:00 a.m. and 6:00 p.m. on days with favourable conditions for insect sampling (i.e., sunny or partly cloudy days, winds no stronger than 30 km/h, temperature above 15°C).

Hover flies within 2.5 m of the transect line were collected using a sweep net during a 20-min walk at an approximate speed of 5 m per minute. Each hover fly's pre-capture behaviour (hovering or visiting) was recorded, and the plant it interacted with was identified. The timer was stopped as soon as an interaction was noticed and remained paused for as long as the interaction, posterior capturing of the hover fly and data collection lasted; thus, the time spent in some sites was sometimes as long as 110 min. Care was taken not to disturb hover flies with our shadows or net while conducting the surveys by walking at a very slow pace along the 100-m transect. Hovering was defined as stationary flight above a flower patch (0.01–0.5 m) and visiting as direct contact with a flower for more than 1 s. Out of the 199 interactions recorded, 92 were removed from the analyses because the sex of the hover flies could not be determined.

Post-collection, hover flies were identified to genus by an expert in the field using a series of unpublished dichotomous keys.

2.2 | Morphometric Measurements

Three measurements were taken for all specimens: dry weight, intertegular span and tibia length. Dry weight was measured using a digital precision scale, while the intertegular span and tibia length were measured using a Leica dissection microscope. Hover flies in the genus *Melangyna* were sexed by inspecting the specimens under the microscope (in males, the eyes meet at the top of the head [i.e., holoptic condition], while the eyes of females are separated [i.e., dichoptic condition; Rotheray and Gilbert 2011]). All specimens were pinned and are deposited in the entomological collection at the University of Sydney.

2.3 | Statistical Analyses

Statistical analyses were conducted using R (R Core Team 2021). We used the 'cor.test' function to create a correlation matrix for the morphometric variables and test for correlations. A principal components analysis was run on these variables using the 'princomp' function. Given the significant correlation between 'intertegular span' and 'tibia length', principal component 1 (PC1) was interpreted as 'size'. An ANOVA was run on 'PC1' for male vs. female individuals using the 'aov' function to test if males were larger than females.

3 | Results

We surveyed hover fly and plant interaction for approximately 7200 min. Our year-long study recorded 106 interactions between Melangyna hover flies and 39 plant species (Figures 1 and 3). Interactions were seasonally distributed, with the majority ($n = 61$; 58%) occurring in winter (Figure 2). We observed two interaction types: hovering ($n = 82$; 77% of total observations) (Figure 2 and Table 1) and flower visits ($n = 24$; 23%) (Figure 3 and Table 2). Of the hovering interactions, ($n = 59$; 72%) were by males and ($n = 23$; 28%) by females.

The plant species with which *Melangyna* had more hovering interactions was *Pittosporum undulatum* ($n = 8$; 7%), followed

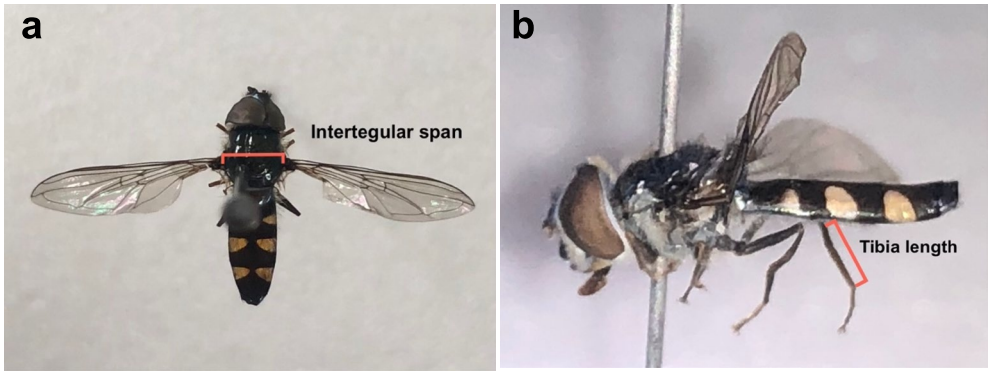

FIGURE 1 | Pinned specimens of *Melangyna*. (a) Intertegular span was measured between the tegulae (i.e., where the wings attach to the body if the hover fly); (b) Tibia length was measured in the left hind leg.

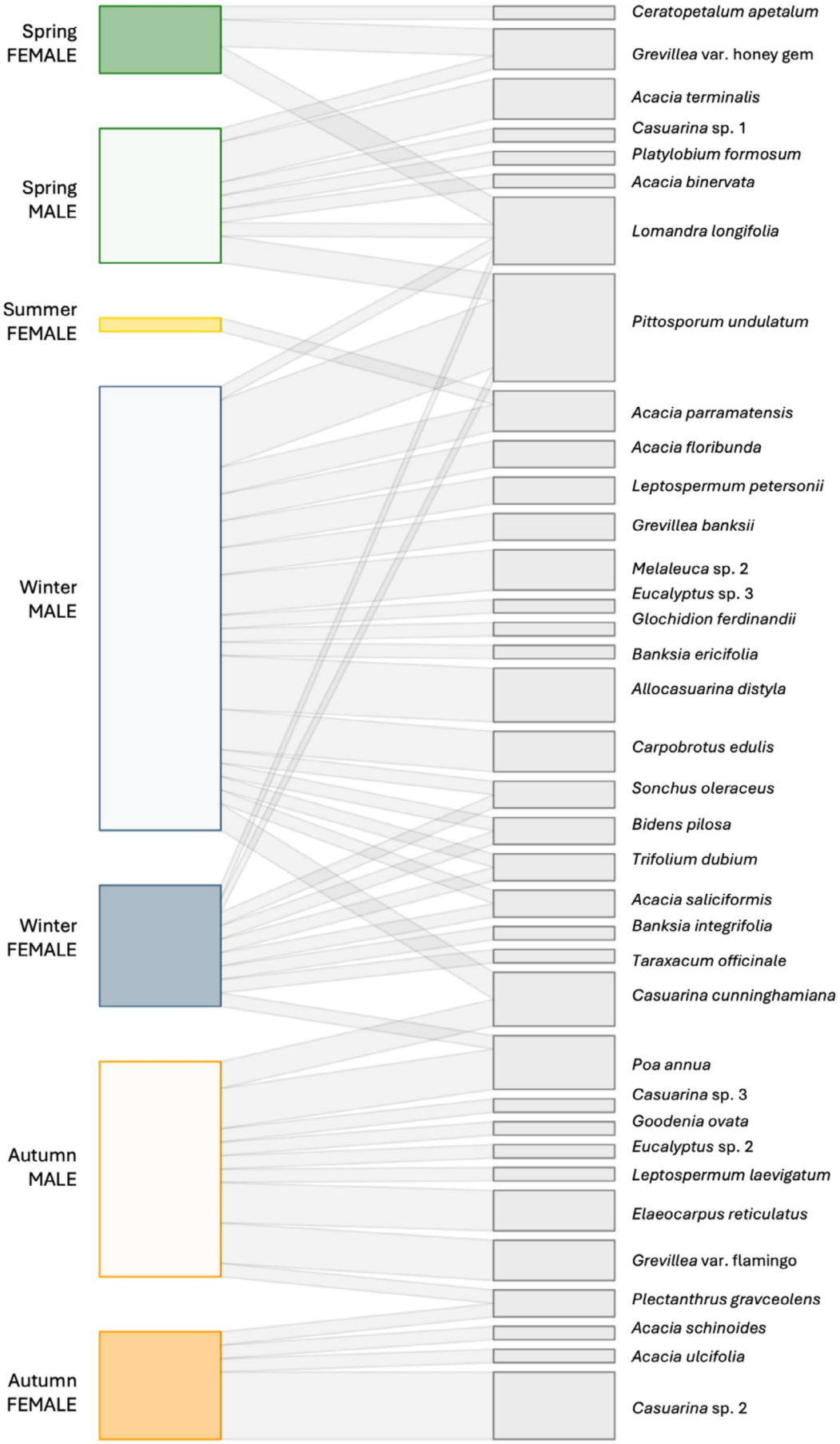

FIGURE 2 | Legend on next page.

FIGURE 2 | Observed hovering interaction networks between female and male Melangyna and plants. The boxes in the left represent the hover flies during different seasons (green = spring, yellow = summer, blue = winter and orange = autumn). The dark-coloured filled boxes represent females, and the light-coloured filled boxes represent males. The polygons between the left and right boxes in each panel represent the strength of interaction, such that thicker polygons represent a higher number of hovering interactions. The boxes at the right represent the plant species.

TABLE 1 | Total number of hovering interactions between *Melangyna* and plants by season and sex.

	Winter		Spring		Summer		Autumn	
Plant species—Hovering	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**
Carpobrotus edulis (L.) N.E.Br.	—	3	—	—	—	—	—	—
Bidens pilosa L.	1	1	—	—	—	—	—	—
Sonchus oleraceus L.	1	1	—	—	—	—	—	—
Taraxacum officinale F.H.Wigg.	1	—	—	—	—	—	—	—
Allocasuarina distyla (Vent.) L.A.S.Johnson	—	4	—	—	—	—	—	—
Casuarina cunninghamiana Miq.	—	2	—	—	—	—	—	2
Trifolium dubium Sibth.	1	1	—	—	—	—	—	—
Lomandra longifolia Labill.	1	1	2	1	—	—	—	—
Acacia floribunda (Vent.) Willd.	—	2	—	—	—	—	—	—
Acacia parramattensis Tindale	—	2	—	—	1	—	—	—
Acacia salicina Lindl.	1	1	—	—	—	—	—	—
Eucalyptus sp. 3	—	1	—	—	—	—	—	—
Leptospermum petersonii F.M.Bailey	—	2	—	—	—	—	—	—
Melaleuca sp. 2	—	3	—	—	—	—	—	—
Glochidion ferdinandi (Müll.Arg.) F.M.Bailey	—	1	—	—	—	—	—	—
Pittosporum undulatum Vent.	1	5	—	2	—	—	—	—
Poa annua L.	1	—	—	—	—	—	—	3
Banksia ericifolia L.f.	—	1	—	—	—	—	—	—
Banksia integrifolia L.f.	1	—	—	—	—	—	—	—
Grevillea banksii R.Br.	—	2	—	—	—	—	—	—
Casuarina sp. 1	—	—	—	1	—	—	—	—
Casuarina sp. 2	—	—	—	—	—	—	5	—
Ceratopetalum apetalum D.Don	—	—	1	—	—	—	—	—
Platylobium formosum Sm.	—	—	—	1	—	—	—	—
Acacia binervata DC.	—	—	—	1	—	—	—	—
Acacia terminalis (Salisb.) J.F.Macbr.	—	—	—	3	—	—	—	—
Grevillea banksii × *pteridifolia* cult. 'Honey Gem'	—	—	2	1	—	—	—	—
Casuarina sp. 3	—	—	—	—	—	—	—	1
Goodenia ovata Sm.	—	—	—	—	—	—	—	1
Elaeocarpus reticulatus Sm.	—	—	—	—	—	—	—	3
Plectranthus graveolens R.Br.	—	—	—	—	—	—	1	1
Acacia schinoides Benth.	—	—	—	—	—	—	1	—
Acacia ulicifolia (Salisb.) Court	—	—	—	—	—	—	1	—
Eucalyptus sp. 2	—	—	—	—	—	—	—	1
Leptospermum laevigatum (Gaertn.) F.Muell.	—	—	—	—	—	—	—	1
Grevillea sp. cult. 'Flamingo'	—	—	—	—	—	—	—	3

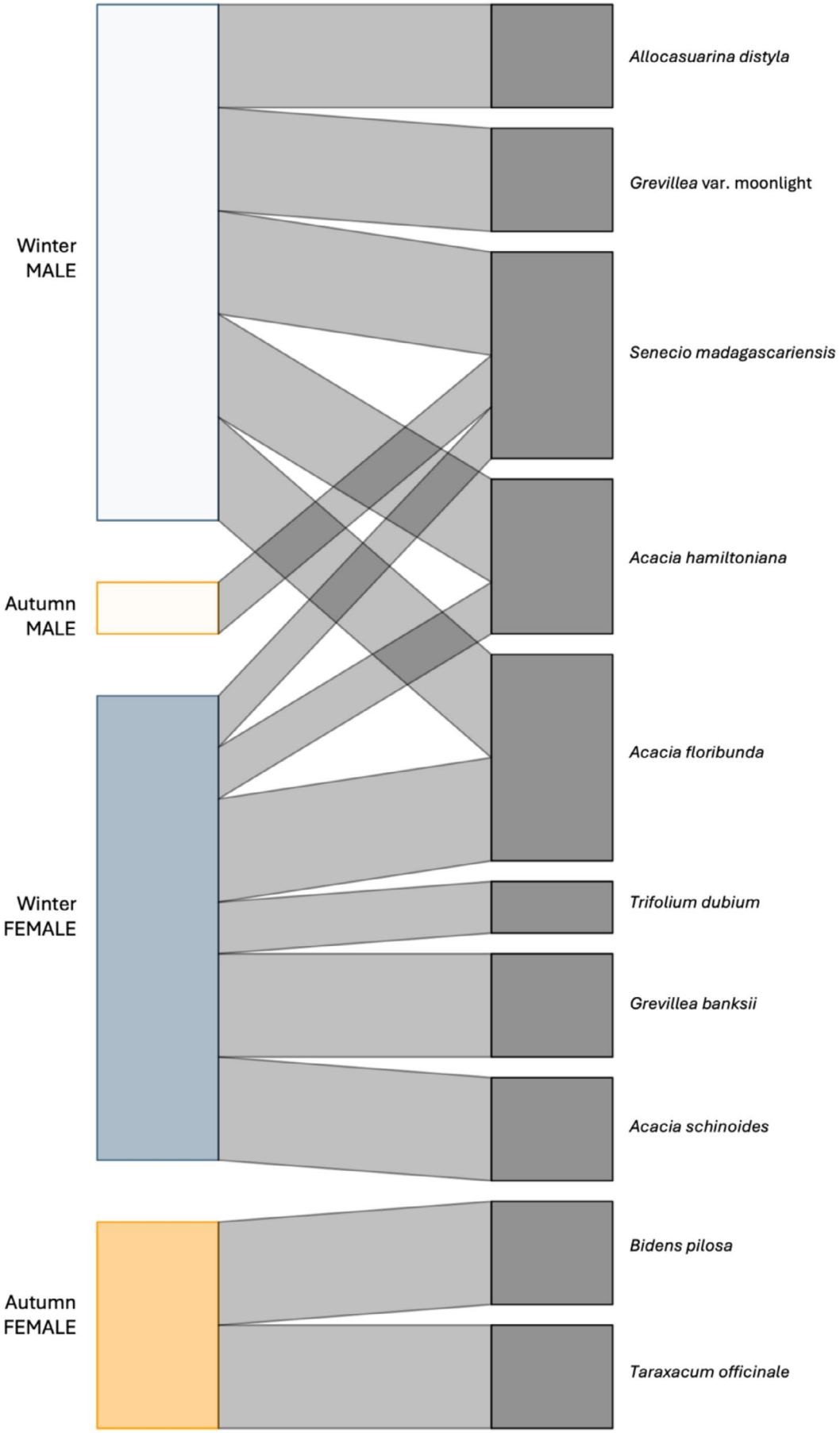

FIGURE 3 | Legend on next page.

FIGURE 3 | Observed visitation interaction networks between female and male Melangyna and plants. The boxes in the left represent the hover flies during different seasons (blue = winter and orange = autumn). Note that there are no visiting interactions for spring or summer. The dark-coloured filled boxes represent females, and the light-coloured filled boxes represent males. The polygons between the left and right boxes in each panel represent the strength of interaction, such that thicker polygons represent a higher number of visiting interactions. The boxes at the right represent the plant species. All plants visited by hover flies were flowering at the time of the visit.

TABLE 2 | Total number of visiting interactions between *Melangyna* and plants by season and sex. All plants visited by hover flies were flowering at the time of the visit.

	Winter		Spring		Summer		Autumn	
Plant species—Visit	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**
Bidens pilosa L.	—	—	—	—	—	—	2	—
Taraxacum officinale F.H.Wigg.	—	—	—	—	—	—	2	—
Allocasuarina distyla (Vent.) L.A.S.Johnson	—	2	—	—	—	—	—	—
Trifolium dubium Sibth.	1	—	—	—	—	—	—	—
Acacia floribunda (Vent.) Willd.	2	2	—	—	—	—	—	—
Grevillea banksii R.Br.	2	—	—	—	—	—	—	—
Acacia schinoides Benth.	2	—	—	—	—	—	—	—
Senecio madagascariensis Poir.	1	2	—	—	—	—	—	1
Acacia hamiltoniana Maiden	1	2	—	—	—	—	—	—
Grevillea banksii × *whiteana* cult. 'Moonlight'	—	2	—	—	—	—	—	—

TABLE 3 | Number of unique plants male and female *Melangyna* interacted with during the four seasons sampled. Interactions are divided into hovering (above) and visiting (below).

		Winter		Spring		Summer		Autumn	
Interaction type	**Description**	***n***	**%**	***n***	**%**	***n***	**%**	***n***	**%**
Hovering	Number of plants *males* interacted with	11	56	5	63	0		5	56
	Number of plants *females* interacted with	3	15	1	13	1	100	2	22
	Number of plants males and females interacted with	6	30	2	25	0		2	22
Visiting	Number of plants *males* interacted with	2	25	0		0		1	34
	Number of plants *females* interacted with	3	38	0		0		1	34
	Number of plants males and females interacted with	3	38	0		0		1	34

by *Casuarina* sp. 2 ($n = 5$; 5%) and *Lomandra longifolia* ($n = 5$; 5%) (Table 1). The plant species with which *Melangyna* had more visiting interactions were *Acacia floribunda* ($n = 4$; 4%) and *Senecio madagascariensis* ($n = 4$; 4%), followed by *Acacia hamiltoniana* ($n = 3$; 3%) (Table 2).

Both the abundance and the ratio between female and male Melangyna varied among seasons. The highest *Melangyna* abundance was in winter (F:M ratio ~ 1:2.5), followed by autumn (F:M ratio ~ 1:3), spring (F:M ratio ~ 1:2) and summer (F:M ratio ~ 1:0). Males hovered over more unique plants than females in all seasons (Table 3). Only one female interaction with a flower was recorded in summer (Table 3).

3.1 | Morphometric Measurements

We measured 133 *Melangyna* individuals, with males comprising 66% of the sample. Intertegular span and tibia length were significantly correlated (r (123) = 0.382, $p < 0.001$), while mass was not correlated to either. 'PC1' was interpreted as 'size', with males significantly larger than females ($F_{(1,123)} = 9.938$, $p = 0.002$) (Figures 4–6).

4 | Discussion

Our study suggests seasonal differences in hovering and foraging behaviours between sexually dimorphic male and female

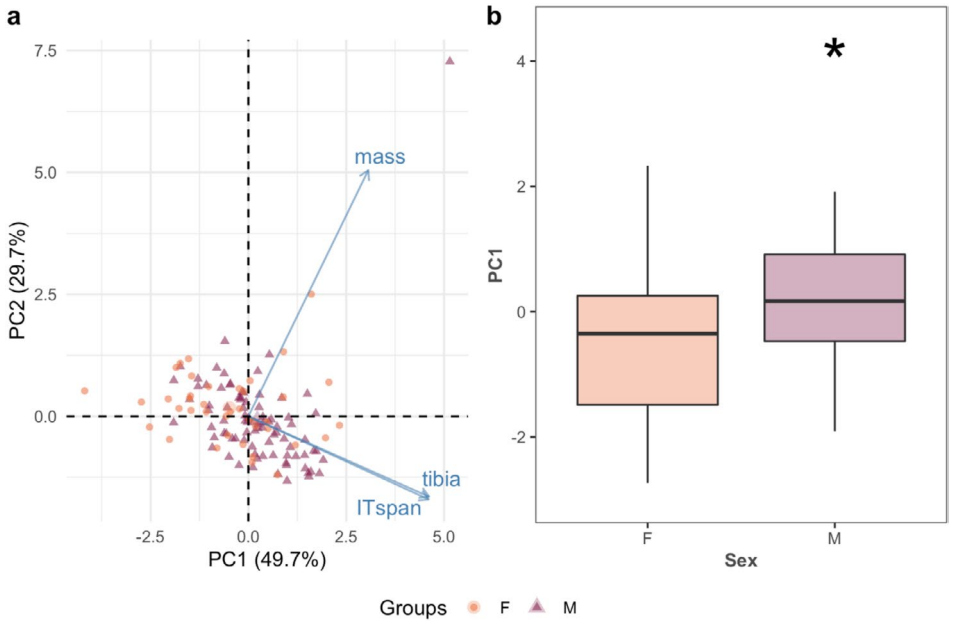

FIGURE 4 | Summary of the morphometric measurements taken to 133 *Melangyna* individuals; female ($n = 67$; 50%), male ($n = 66$; 50%). (a) Biplot representing the observations (orange dots = females; purple triangles = males) and variables (blue arrows) of the principal component analysis. Principal component 1 (PC1) is depicted in the x-axis and represents 49.7% of the proportion of the variance among the components. Principal component 2 (PC2) is depicted in the y-axis and represents 29.7% of the variance among the components. (b) Comparison of PC1 between female (F) and male (M) individuals; bars range from the value at the 75th to the upper value within 1.5 times the inter-quantile range or 25th to the lower value within 1.5 times the inter-quantile range. PC1 (representing hover fly size) is significantly higher in males than in females ($F(1,123) = [9.938]$, $p = 0.002$); '*' denotes a significant difference between groups.

FIGURE 5 | Melangyna hovering near flowers of an onion weed (Nothoscordum gracile). Photo Marcus Johnson.

FIGURE 6 | Melangyna visiting the flowers of a prickly-leaved paperbark (Melaleuca nodosa). Photo Manuel Lequerica Tamara.

Melangyna hover flies, which may indicate the partitioning of floral resource use among behaviours and sexes. These observations generate a suite of hypotheses that are central to further understanding the influence on the ecology of this prominent group of pollinators.

Hovering was a more common behaviour than direct visiting of flowers, with considerable resource overlap during this exploratory behaviour. Males hover when foraging or defending territories (Mutin 1996; Rotheray and Gilbert 2011), while females hover when foraging, searching for mates or seeking oviposition sites (Dixon 1958). Given these broad uses, it is expected that males and females use the same species of plants when exploring their habitats and there are significant opportunities to examine how the different motivations for hovering behaviour influence plant selection.

During our study, different individual hover flies visited the same species of plants, although this varied among seasons and also between sexes. It is possible that seasonal differences are due to differences in flower availability, while sexual variations may be explained by metabolic differences (Dixon 1958; Rotheray and Gilbert 2011). Although both sexes require the carbohydrates from nectar to fulfil their energetic requirements, females have

a higher amino acid requirement related to gestation and oviposition (Soleyman-Nezhadiyan 1996; Schneider 1969; Hickman et al. 1995; Branquart and Hemptinne 2000). Despite extensive sampling (~120 h), many hover flies were observed flying rather than interacting with floral resources. Although some studies have explored indirect evidence of flower visitation, such as pollen grains on the body surface, mouth parts (Gilbert 1981) or inside the gut (Haslett 1989; Soleyman-Nezhadiyan 1996), these have been limited to short periods of time. Future studies with increased sampling effort should consider exploring the differences in flower visitation during an entire year to increase our understanding of seasonal dietary preferences and changes.

Although some male and female hover flies visited unique flowers during our study, the flowers visited by males were not particularly nectar-rich, nor were the flowers exclusively visited by females pollen-rich. Instead, both males and females visited flowers that offer copious nectar (such as *Grevillea* spp. and *Banksia* spp.) as well as plants that offer copious pollen (such as *Acacia* spp. and male individuals of *Casuarina* spp. and *Allocasuarina* spp.). It has been suggested that larger male body size leads to a preference for energy-rich nectar (Peters 1983; Jervis et al. 1993), while smaller females, needing additional protein for egg production, tend to forage on pollen (Gilbert 1985; Wheeler 1996). This sexual size dimorphism could be a result of sexual selection (where bigger males have an advantage in male–male combats) or intraspecific niche divergence (where the utilisation of different niches by males and females results in morphological differences) (Shine 1989). Irrespective of its evolutionary origin, sexual dimorphism in *Melangyna* may impact ecological processes like pollination (Roswell et al. 2019). For example, smaller flowers may exclude hover flies with larger body sizes (i.e., males) from accessing their resources (Jervis et al. 1993), thus it is important to investigate these elements in conjunction in the future.

The abundance of *Melangyna* is highest during the colder months of the year, a time when several abundant native plants flower but when few native insects are active, which suggests that *Melangyna* and these winter-flowering plants may have an interesting yet understudied historic insect–plant association. Understanding what drives intraspecific floral preferences in *Melangyna*, and if the sexual dimorphism of these hover flies has consequences for the reproduction of winter-flowering plants are important questions to advance our biological knowledge on this charismatic group of floral visitors and our understanding of these important insect–plant interactions.

Author Contributions

Manuel E. Lequerica Támara: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, software, visualization, writing – original draft, writing – review and editing. **Tanya Latty:** conceptualization, methodology, supervision, writing – review and editing. **Caragh G. Threlfall:** conceptualization, formal analysis, investigation, methodology, supervision, validation, writing – review and editing. **Dieter F. Hochuli:** conceptualization, formal analysis, funding acquisition, methodology, project administration, resources, supervision, validation, writing – review and editing.

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Disclosure

This manuscript is part of the PhD thesis titled 'The ecology and behaviour of hover flies in urban ecosystems', published in the online institutional repository of The University of Sydney Library: https://hdl.handle.net/2123/29985.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Our data are archived in The University of Sydney repository and will be made available at the time of publication (or upon request).

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