Apidologie (2022) 53:49
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https://doi.org/10.1007/s13592-022-00951-4

Original article

Nearly half of spring-flying male *Andrena* bees consume pollen, but less than female conspecifics

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Received 22 February 2022 – Revised 17 July 2022 – Accepted 18 July 2022

Abstract – Despite its potential nutritional benefits, consumption of pollen by adult solitary bees has rarely been quantified. Pollen consumption by adult male bees is usually assumed to be negligible, but few studies have investigated this assumption. Here, we review existing literature on adult male bee pollen consumption and present new data on female and male pollen consumption by 9 species from 5 subgenera of spring-flying *Andrena*. We dissected and plated full contents of the digestive tract, calculating body-size adjusted pollen volumes for each bee. More females had consumed pollen than males (87% compared to 46%, respectively). Of the bees with pollen, females had consumed over nine times more pollen. However, 10% of males had consumed over 10,000 pollen grains and the highest two exceeded 30,000 grains. Given the large proportion of male bees that consumed pollen, we suggest future work should explore daily/seasonal patterns of consumption and possible fitness implications.

***Andrena* / Male bees / Pollen consumption / Pollen counts / Pollen volume / Intertegular distance**

1. INTRODUCTION

Adult feeding in insects is highly variable. In many taxa, adulthood is a relatively brief lifestage primarily for reproduction and dispersal (e.g., Lepidoptera and Diptera reviewed in Wäckers et al. 2007; Ephemeroptera, Sartori and Brittain 2015), while others with energetically intensive adult stages actively forage as adults (e.g., Odonata, Baird and May 1997; Coleoptera, Wäckers et al. 2007). Within Hymenoptera, adult feeding in parasitoid wasps is often associated with greater longevity, but usually only considers sugar sources like honey, sucrose, or honeydew (e.g., Siekmann et al. 2001). In contrast, protein-rich pollen consumption by bees as adults has been suggested as a synapomorphy of the clade (Michener 2007). Female solitary bees collect large amounts of pollen from flowers to create mass brood provisions for their offspring (Danforth et al. 2019). Adult bee pollen consumption for their own physiological maintenance remains poorly understood, and particularly so for male bees.

Adult female solitary bees continue to produce eggs throughout their adult lives (Cane 2016) which requires a constant supply of the proteins and lipids in pollen (Cane et al. 2017). This has been demonstrated in female *Osmia californica,* who use this pollen as a source of protein for egg development and proper oocyte maturation (Cane 2016; Cane et al. 2017). Similarly, egg and yolk development in *Megachile rotundata* is dependent on pollen (Richards 1994). A few studies explore the timing of these

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Manuscript editor: Cedric Alaux

female adult meals. Female *Melissodes rustica* consume pollen after each day's single cell is provisioned, and occasionally smaller amounts earlier in the day (Isenberg et al. 1997). Similar "feeding trip" behavior has been observed in *Calliopsis persimilis*, several *Perdita* species (Danforth 1989, 1990, 1991), and female *Nomia melanderi* who also make daily foraging trips after the day's brood provisioning (Cane et al. 2017; solitary female consumption also reviewed here).

Less is known about adult male solitary bee pollen consumption. Anecdotally, male *Macropis fulvipes* have been observed consuming *Lysimachia* pollen (Schäffler and Dötterl 2011), and pollen has been found in adult male guts of multiple megachilid genera (Käpylä 1978, Dobson et al. *unpubl. data*). One 1956 study dissected males and females of 40 species of solitary bees; despite low sample sizes per species, this study found that male *Andrena* and *Colletes* more often had pollen than other genera (Taniguchi 1956). Taniguchi classified some pollen consumption as purely incidental during "nectar-sucking" behavior, while suggesting that other species with larger amounts of pollen had intentionally consumed it (Taniguchi 1956). The degree to which male pollen consumption is incidental rather than intentional or physiologically necessary remains unclear. Male bees certainly have ample opportunity to consume pollen if they choose to: adult male solitary bees visit multiple flowers and often externally carry more diverse pollen types than female conspecifics (Cullen et al. 2021). They also have distinctly dissimilar floral preferences from conspecific female bees, however, are far less likely to visit a nectar-less flower, suggesting males primarily forage for nectar (Roswell et al. 2019).

The possibility that male bees consume pollen is an important knowledge gap, since pollen consumption could potentially improve male fitness, e.g., if protein-rich sperm benefits from adult pollen consumption. There is scattered evidence of pollen consumption with possible fitness effects in social male bees, although the majority of these studies only explore the impact of colony-level pollen access while males are larvae. In these studies, males reared with access to more or higher quality pollen had greater size and fitness metrics as adults (e.g., greater individual survival (McAulay and Forrest 2019), larger heads (Lawson et al. 2020), longer wings and survival (Regali and Rasmont 1995), earlier day with peak sperm counts (Pech-May et al. 2012), higher sperm viability (Rousseau and Giovenazzo 2016), and body weights (Czekońska et al. 2015; Rousseau and Giovenazzo 2016; Szentgyörgyi et al. 2016); see Supplemental Table 1). In terms of adult male consumption, Szolderits and Crailsheim found that adult male *Apis mellifera* consume pollen at least for the first four days of adulthood (1993). Stürup et al. found that adult honey bee males living in host colonies with or without pollen access had no differences in sperm viability after 12 days, although they did not examine whether any males had directly eaten pollen or not (2013).

Beyond basic physiological maintenance, there are reproductive functions in both social and solitary male bees that could potentially benefit from adult protein intake. Although spermatogenesis in *Apis mellifera* males occurs during the pupal stage and no new sperm are made after eclosion (Snodgrass 1910; Bishop 1920; Lago et al. 2020; Slater et al. 2021), in many species the sperm do not fully migrate to the seminal vesicles until at least several days and up to a few weeks post-emergence (*Apis mellifera* Snodgrass 1910; Bishop 1920; *Friesella schrottkyi* Brito et al. 2009; *Osmia cornuta* Strobl et al. 2019; *Scaptotrigona xanthotricha* Araújo et al. 2020). Other stages of sexual maturation and sperm viability are only completed after eclosion, like seminal fluid production (Slater et al. 2021), and protein content of the accessory mucus gland which is used to ensure that sperm is not refluxed after copulation (Colonello and Hartfelder 2003). These functions suggest that post-eclosion sperm maturation in social bees could benefit from protein and lipid supplementation, potentially via pollen consumption.

Solitary males, which may create less total sperm than *Apis* (e.g., *Osmia cornuta,* Strobl et al. 2019), have also been thought to eclose with their full sperm complement (Araújo et al. 2010). However, shortened seminiferous tubules in certain species have been interpreted as evidence of continued adult sperm production by *Xylocopa* (Ferreira et al. 2004). In a study of solitary *Centris* sp., the authors interpreted a lack of certain epithelial structures as a differentiation from social bees who eclose with all of their sperm (Gomes et al. 2012). The testicular tubules of adult *Hypanthidium foveolatum* were reported to contain sperm at various stages of maturation (Gracielle et al. 2009). Thus, at least some solitary species may consume pollen as adults for both sperm production and/or maturation, but these possible mechanisms need further study.

Before investigating the fitness effects of pollen consumption, we must first understand how much pollen male solitary bees consume. Here, we review the literature and then formally quantify male pollen consumption in nine spring-flying *Andrena* species and compare it to conspecific female pollen consumption. We focus on bees in the genus *Andrena,* which have similar life histories to many solitary bees. For example, *Andrena* are central place foragers with a single female foundress, are mass provisioning, and males emerge phenologically before their female counterparts (Danforth 2019). The nine species studied here also represent a range of life histories and nesting habits. For example, *A. carlini* nest in isolation (Schrader and LaBerge 1978), while *A. dunningi* nest in aggregations (Johnson 1981), and consume pollen from a wide diversity of plants (Wood and Roberts 2017). Thus, *Andrena* are important for both their economic and ecological roles (Park et al. 2016; Blitzer et al. 2016), and may provide a window into male solitary bee behavior more broadly. As most studies assume male bees do not consume meaningful quantities of pollen, we similarly predicted that most male *Andrena* guts would hold little pollen relative to female conspecifics, but that some *Andrena* may eat non-negligible amounts of pollen (e.g., Taniguchi 1956).

2. METHODS

2.1. Literature review

We conducted a literature review for any evidence of pollen consumption among male bees and any evidence that pollen consumption impacted metrics of male fitness on Web of Science and SCOPUS. Our criteria required that the study *either* (a) directly observed or measured male pollen consumption *or* (b) manipulated pollen availability and included at least one response variable such as male bee size, survival, fitness, or other metric(s) including reproduction or proxies for reproduction. Several different search strings were attempted including "male" AND "pollen" AND "Apoidea OR bee" AND "reproduct* OR fitness OR body size OR weight OR sperm." This particular search, for example, resulted in 378 results in Web of Science Core Collection and 208 results in Scopus database, yet title and then abstract review on Oct 12, 2021 revealed only 3 relevant studies in Web of Science and 0 studies returned in Scopus. We thus expanded our search to also include papers found via citation-mining, personal communication, and expert knowledge. Although less systematic, this pathway is appropriate for narrowly focused topics where the relevant results are only recorded incidentally rather than as the focus of a study, and thus not easily found via keywords or search terms.

2.2. Bee sampling and gut pollen quantification

Sampling was completed by pan trapping in the Finger lakes region of New York State in the spring of 2018 and 2019, in nine orchards and adjacent forest sites as part of a larger study (Urban-Mead et al. 2021). Briefly, five traps were set in the canopy (20-25 m), understories (< 1 m), and orchards (in flowering branches) at all sites and collected every 7–10 days from March through the first week of June (Urban-Mead et al. 2021). All bees were collected from pan traps directly into Whirl-pak™ bags with 95% ethanol (Urban-Mead et al. 2021). *Andrena* species were subset from this larger dataset for inclusion in this study if we had collected at least 10 bees per sex.

Before being pinned and labeled, bee abdomens were carefully opened with forceps to maintain their integrity for later species identification (for species identification, see Urban-Mead et al. 2021). The entire digestive tract of crop, ileum, midgut, and rectum (hereafter, "gut") was removed from the body and forceps were used to mix and spread the pollen grains as evenly as possible across the slide area. Pollen was dyed with Calberla solution for visualization. A bee was considered to have "no pollen" if there were <30 grains visible across the entire slide at this stage (Harmon-Threatt and Kremen 2015; McArt et al. 2017). We calculated the number and proportion of each species with pollen. Then, from among bees "with pollen," five female bees were selected semi-randomly from available bees to maximize variation across sites and dates. Ten male bees, which were more numerous, were randomly selected from remaining bees with function stratified in Rpackage *splitstackshape* (Mahto 2019). The stratified command randomly selects within a grouping variable, in this case bee species.

The nine *Andrena* species used in this study were the following: *Andrena (Andrena) mandibularis* Robertson 1892*, A. (A.) tridens* Robertson 1902, *A. (Melandrena) carlini* Cockerell 1901, *A. (Melandrena) dunningi* Cockerell 1898, *A. (Melandrena) pruni* Robertson 1891, *A. (Scrapteropsis) imitatrix* Cresson 1872, *A. (Simandrena) nasonii* Robertson 1895 *A. (Trachandrena) rugosa* Robertson 1891, and *A. (Tylandrena) perplexa* Smith 1853.

A compound Olympus BX41 microscope was used with the software CellSens© to quantify relative gut pollen counts and measure pollen dimensions at 200 × magnification. A random number generator was used to select the transect at which to begin counting (McArt et al. 2017; Russo and Danforth 2017), and every grain of each morphotype in the field of vision was counted across a full transect pass. This was repeated for 10 total randomly initiated transects with no transects repeated. Bee intertegular distances, a common proxy of bee body size (Cane 1987; Greenleaf et al. 2007; Kendall et al. 2019), were measured with the tool from cellSens software on an Olympus SZX10 stereo microscope (Olympus Corp. Tokyo, Japan). Pollen grains were categorized into pollen morphospecies groups based on the lowest possible taxonomic resolution (Urban-Mead et al., *in revision*), and simple richness of pollen morphogroups eaten was calculated for each bee.

2.3. Pollen volume standardization

We calculated absolute pollen counts, volumes, and body-sizes to arrive at body-size adjusted pollen volumes for each bee in our dataset (Fig. 1). Because we expect gut volume to scale with body size volume, we adjust for body size to understand if consumption is varies separately from expected size-based variation. The *Andrena* species in our sample vary in body size among species, and male *Andrena* are consistently smaller than their female conspecifics.

First, to convert pollen counts to volumes (Buchmann and O'Rourke 1991), we measured the polar and orbital diameter of each pollen morphotype from a subset of 300 grains of pollen from each slide. A morphotype's pollen volume was calculated using standard sphere or ovoid volume formula, depending on the morphotype shape (Buchmann and O'Rourke 1991; O'Rourke and Buchmann 1991). Using these morphotype volumes and their relative abundances in the 300 grain subsample, we calculated a weighted average of the pollen grain for each bee's pollen load. We then multiplied this average pollen volume by the total number of pollen grains. Finally, to calculate body-size adjusted pollen volume (e.g., "pollen volume per mm of intertegular distance"), we divided pollen volume by the intertegular distance of each bee.

2.4. Statistical analyses

All statistical analyses were done in R version 4.0.1, "See Things Now." We first calculated the

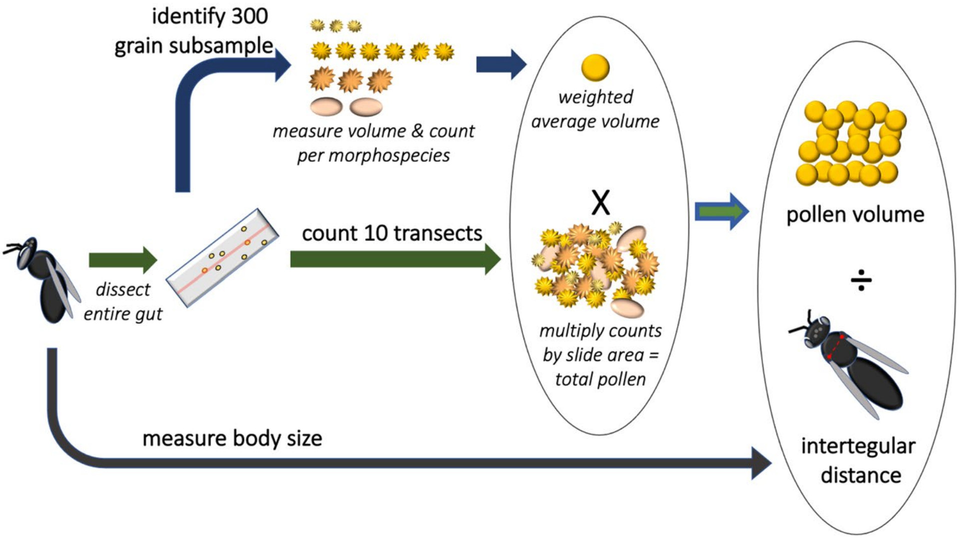

Figure 1. Method diagram for body-size adjusted pollen volume: pollen volume per unit of body size per bee. For each bee included in the study, we counted all pollen grains visible in 10 non-repeating transects randomly initiated along the edge of the microscope. We also identified the first 300 pollen grains obtained in a separate group of random transects, and measured the polar and orbital diameters to allow for a volume estimate per morphospecies. Finally, we measured the shortest distance between the tegula (ITD) of each bee. These three steps allowed us to multiply the pollen counts by the weighted average pollen volume and finally standardize it by body size.

percent of bees with non-zero pollen for each sex and species. We used a Wilcox rank sum test to ask if females had a higher body-size adjusted pollen volume than males overall. Next, we built several linear models with similar structures in Rpackage *lme4* (Bates et al. 2015). In all models, the response was body-size adjusted pollen volume; a log transformation was applied due to non-normality of the residuals. In the first model, we asked if sex or species predicted total body-size adjusted pollen volume in the gut. The interaction of species and sex were set as fixed effects; the interaction was not significant ($F_{1,8} = 1.38$, $p = 0.21$), so we ran the model again with species and sex as fixed effects without the interaction term. We then asked if body-size adjusted pollen volume was predicted by the Day of Year and the interaction of sex and body size; in this model we, included Species as a random effect to allow the intercept to vary among species. Due to an interaction between sex and body size, we also built separate models for each sex with body size as a fixed effect and Species as a random effect. For each model, we tested for significance of each fixed effect with a type-III Anova from Rpackage *car* (Fox and Weisberg 2019) and emmeans() (Lenth 2020). Finally, we ran likelihood ratio tests of our hypothesized models described above compared with models containing sampling location (site) as fixed or random effects: site explained no additional variation. For contingency table of bee sampling by site, see Supplementary Table S3.

3. RESULTS

3.1. Literature review

We identified only 7 studies that directly observed or measured adult male solitary bee pollen consumption (Table I). Our literature review also found 11 studies that manipulated pollen availability at the colony or micro-colony level and reported adult male trait responses to pollen availability as larvae (but did

Table I Literature review. Previous studies reporting direct observation or measurements of adult male pollen consumption

Citation	Study description	Species	Findings
(Dobson et al. *unpubl.data*)	Bees were collected at different times of day and season as they returned from foraging trips, and qualitatively visually scored for gut fullness	*Megachile rotundata*	Males ate less pollen than females. Males ate more early in flight season, when over half of bees had 50% full midguts
		Nomia melanderi	Males ate less than females; < 30% of males had midguts at least 50% full
		Chelostoma rapunculi	Males ate less than females, and ate more pollen as the later in the flight season; only 4% with empty midguts in late season)
		Melissodes agilis	Only males measured; 20% of males had midguts more than 50% full
(Figueroa et al. 2021)	Newly emerged bees were either inoculated with *Crithidia bombi* or not, placed into individual containers, and fed either a mixture of sucrose and pollen or just sucrose	*Megachile rotundata*	Pollen access did NOT affect likelihood of infection in males
			Pollen access did NOT affect number of *C. bombi* cells found in male guts
			Pollen access had NO impact on male survival
(Fowler et al. 2020)	Queen, male, and worker bees were inoculated with *Crithidia*, moved to individual containers, and fed either a sunflower pollen mix or a wildflower pollen mix for 7 days	*Bombus impatiens*	Males consumed less pollen than females
			NO relationship between pollen type and *Crithidia* cells in males
(Käpylä 1978)	Digestive tracts of adult bees netted on return from foraging trips. Bees were dissected their guts plated, and up to 200 pollen grains were identified	*Chelostoma maxillosum*	Male and female guts were dominated by *Ranunculus* pollen
		Chelostoma rapunculi	Male and female guts were dominated by *Campanula* pollen
		Chelosstoma campanularum	Female guts were dominated by *Campanula* pollen, while males ate a mix of *Campanula, Potentilla,* and other pollens

Table I (continued)

Citation	Study description	Species	Findings
		Heriades truncorum	Male and female guts were dominated by *Achillea*-type pollen
		Osmia tuberculata	Female guts held a mix of *Convallaria*-type, *Lathyrus*, and other pollens; male guts had *Caragana aborescens, Convallaria*-type, *Vaccinium*, and others
(Schäffler and Dötterl 2011)	Direct flower visitation and pollen consumption observed; digestive tracts not observed	*Macropis fulvipes*	Females and males observed manipulating anthers and eating pollen from flowers
(Szolderits and Crailsheim 1993)	Male bees were collected 0, 1, 2.5, 3, 4, 5, 8, and 20 days post-eclosure and their gut pollen was quantified	*Apis mellifera*	Proteolytic activity in the midgut peaks around 4 days of age Pollen collected from younger males was more digested than pollen collected from older males 3-day-old males had the most pollen in their gut Older males had almost no pollen in their gut Older males had heavier midguts
(Taniguchi 1956)	Male and female bees of various species were netted and dissected, and the pollen content on and in their bodies was quantified Sample sizes in parentheses if provided, otherwise unknown The following *Andrena* were omitted because it was unclear whether result of "large quantity of pollen was found in the stomach" referred to males or females: *A. hebes*, *A. nipponica, A. sasacki*	*Andrena knuthi*	Large quantity of pollen (same as females) in rectum, stomach, and ventriculus of males
		Andrena opacifovea	Pollen found in rectum and ventriculus of most bees. Pollen less than females. A few males (3) had large quantity of stomach pollen but no stomach pollen in most males

Table I (continued)

Citation	Study description	Species	Findings
		Andrena watasei	Males ate a "fairly large amount" of pollen
		Andrena dentata	Males with pollen in rectum and ventriculus. Less pollen than females. Pollen in guts of about half of males
		Andrena foveopunctata	Male (1) had pollen in rectum and ventriculus, while another had none in gut (1)
		Andrena tsukubana	Nectar in rectum and ventriculus of males contained "considerable amount" of pollenmale
		Andrena prostomias	Most males with "abundant" pollen in gut (pollen with nectar), rectum, and ventriculus
		Andrena fukaii	One male with pollen in rectum and ventriculus, but no pollen in the nectar in gut
		Colletes patellatus	"Large quantity" of pollen in gut, rectum, and ventriculus of males
		Colletes collaris	Males (6) with pollen in rectum and ventriculus
		Hylaeus spp.	Males had rectum and ventriculus filled with pollen. Males had "fairly large quantity" of pollen in gut
		Ceratina flavipes	Males had pollen in rectum/ventriculus, much less pollen than females
		Anthophora acervorum villosula	Males had pollen in rectum/ventriculus, less pollen than females. Males had no pollen in nectar stomach
		Anthophora florea	Male (1) had no pollen in gut, rectum, or ventriculus

Table I (continued)

Citation	Study description	Species	Findings
		Tetralonia mitsukurii	Males with pollen in in rectum and ventriculus, less than females
		Tetralonia nipponensis	Males with pollen in rectum, very small amount
		Eucera sociabilis	Males with small amount of pollen in rectum, no pollen in nectar stomach
		Nomada orientalis	Males (2) with no pollen
		Nomada harimensis	Males with no pollen
		Epeolus japonicus	Fresh males (6) with no pollen
		Megachile tsurugensis	Males with no pollen except small amount in rectum in 3 “exceptional cases”
		Megachile nipponica	Males with “some or a little” pollen in rectum
		Osmia cornifrons	Male rectum with "scanty" pollen (1 of 4)
		Osmia pedicornis	No pollen found in males
		Osmia orientalis	No pollen found in males
		Osmia taurus	Pollen found in rectum/ventriculus of some males, less than that of females
		Halictus scitulus	Pollen in rectum in some males. Pollen small in quantity. No pollen in nectar stomach
		Halictus mutilus	Males with no pollen

not measure adult pollen consumption); 9 were of eusocial bees. These studies, which are not intended to be exhaustive of the larval diet manipulation literature, are summarized in Supplemental Table A1.

3.2. Pollen volume by phenology

Consistent with *Andrena* phenology, female bees were captured later than male bees (Supplemental Figure A1). However, Julian day of capture within a species had no effect on volume of pollen eaten (female: $p = 0.48$, male: $p = 0.29$) (Supplemental Figure A2). Also consistent with *Andrena* generally, males were much smaller than conspecific females.

3.3. Pollen volume by sex and species

Across the nine *Andrena* species, 86.98% ± 0.08 of female bees had pollen in their gut (defined as at least 30 grains) compared to 46.3% ± 0.16 of male bees (Fig. 2). The estimated mean number of total pollen grains in female guts was 52,240 ± 7521, compared with 3882 ± 877 pollen grains in male guts. The raw volume before adjustment by body size for females was 4.96E + 09 μm^3 and for male bees was 5.49E + 08 μm^3. Male bees ate larger pollen grains than females (average individual pollen grain volume eaten by males: 2.74E + 05 μm^3, females: 1.03E + 05 μm^3). Female bees overall had higher body-sized adjusted pollen volumes in their guts than male bees (Wilcox rank sum test, $z = -8.05$, $p < 0.001$) and female guts contained 9.33 times more body-size adjusted pollen volume than males (calculated using emmeans). Interestingly, in one case, a male *Andrena dunningi* male bee had eaten a volume of pollen that exceeded the average female pollen gut volume. Total pollen volume differed among *Andrena* species ($F_{1,8} = 3.23$, $p = 0.003$; Fig. 3a), and strongly between sexes ($F_{1,8} = 121.36$,

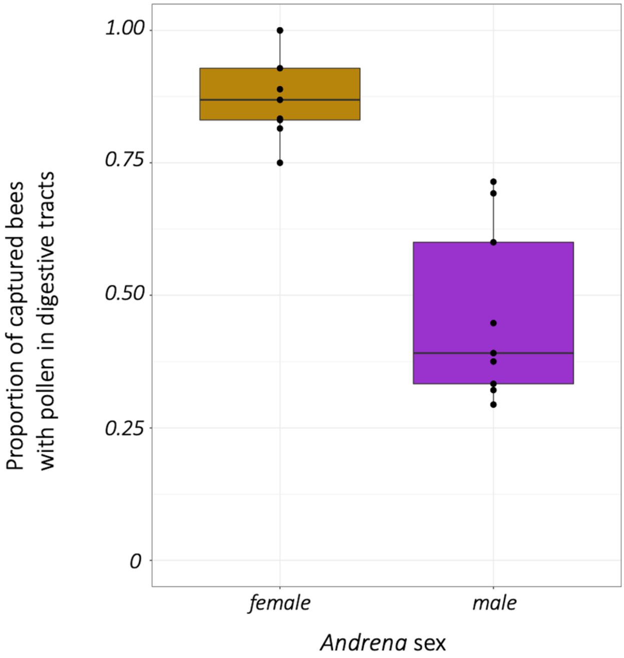

Figure 2. Proportion of all bees of focal species with pollen in their digestive tracts. Bees were classified as having pollen if they had at least 30 grains of pollen. Data are summarized by species, one point per sex per species. Middle lines are median, upper, and lower lines are quartiles; points beyond whiskers represent outliers.

$p < 0.001$; Fig. 3a). When tested separately by sex, we found that body-size adjusted pollen volume per millimeter of body size was positively correlated with body size (ITD) in male bees ($\chi^2_{1,1} = 5.50$, prob($> \chi^2$) = 0.019; Fig. 3b), but found no relationship in females ($\chi^2_{1,1} = 0.53$, prob($> \chi^2$) = 0.47; Fig. 3b). Finally, when all pollen morphotypes were summed, male bees were more likely than females to have five or more pollen types in their guts; male diets usually had fewer pollen grains but more pollen morphotypes (Fig. 4). When sex, species, Day of Year, and body size were all included in a single universal model, Day of Year was not significant and all other results were qualitatively the same (for full model output, see Supplemental Table 2).

4. DISCUSSION

Consistent with our expectations, female bees were more likely than males to have pollen in their guts and on average consumed over nine times more pollen than males. However, the number of male bees that consumed substantial quantities of pollen suggests at least occasional consumption beyond incidental contact during nectaring. This reveals a previously unexplored aspect of wild bee biology and opens new questions regarding the importance of pollen for adult male solitary bees. This topic is likely understudied due to the assumption—based primarily on *Apis mellifera*—that male bees eclose with their full complement of sperm and thus have no adult need for pollen. However, some literature indicates that sperm quality and quantity can improve via adult male pollen consumption and may additionally be useful for general physiological maintenance and repair.

Female *Andrena* overall consumed more pollen than males after adjusting for body size. We found no relationship between female body size and the pollen consumed per millimeter of body size; that is, female *Andrena* of different sizes consumed similar amounts of pollen for their size. We cannot rule out that we may have simply failed to detect an existing pattern due to non-standard times of day of sampling and low

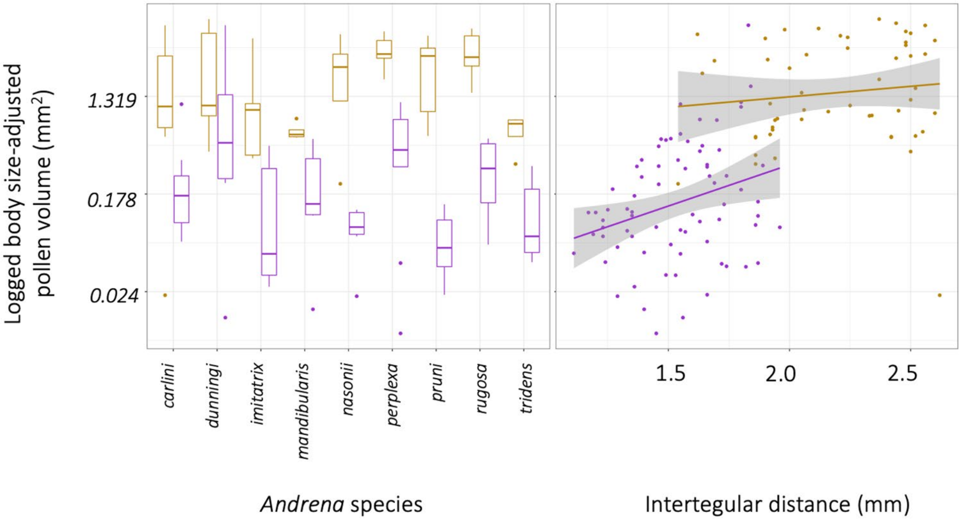

Figure 3. Standardized pollen volume by species and sex. Left: Pollen counts were adjusted by weighted average pollen morphospecies's volumes and divided by the bees' body size. Middle lines are median, upper and lower lines are quartiles; points beyond whiskers represent outliers. Right: The same response variable with body size (intertegular distance) on the x-axis. Note y-axis is on a log scale. For the same left-hand panel by Subgenus and Sex, please see Supplemental Figs. A3 and A4.

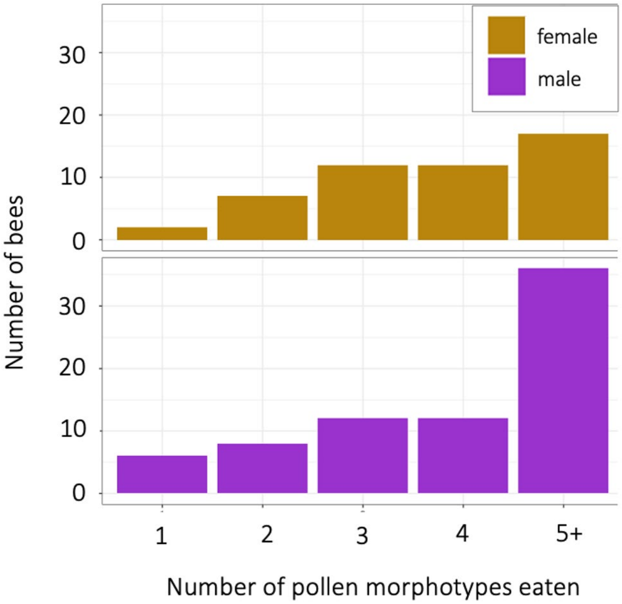

Figure 4. Histogram of number of pollen morphotypes eaten by male and female *Andrena* who had consumed pollen. We note that these raw richness counts could include very small numbers of grains, including pollen consumed incidentally.

numbers of females counted per species. We did, however, find that male body size was positively correlated with pollen consumption per millimeter of body size. The several individual males who had eaten the largest pollen meals were *A. carlini*, *A. dunningi*, and *A. perplexa*, and had body sizes comparable to many of the mid-size female bees of other species measured in this study (we note that *Andrena* males are smaller than conspecific females). In general, larger solitary female bees lay larger eggs (Danforth 2019), and male body size frequently has important ecological implications in other bee genera. For example, in *Hylaeus alcyoneus* and *Amegilla dawsoni*, where males exhibit extreme size variation, larger males are known to exclude smaller males from floral resources (Danforth 2019). Preliminary work suggests that pollen consumption may increase male vigor and the number of successful mating events (Dobson, HE *unpubl.data*), but not sperm counts (Dobson, HE and Welter, M, *unpubl.data*). This is a possible exciting avenue for future research; to our knowledge there are no published studies of no fitness implications of pollen use for adult solitary males.

We found that male bees were more likely to consume more than five pollen morphotypes, which is consistent with prior work finding male solitary bees visit a higher diversity of flowers than females (Roswell et al. 2019; Cullen et al. 2021). Differences in the diversity of male and female pollen consumption may be influenced by the time-of-day bees collect pollen for consumption (sensu Cane et al. 2017). While several species of solitary females make one trip at the end of the day to collect pollen for consumption (Danforth 1990; Cameron et al. 1996), male bees of all species are assumed to consume pollen opportunistically. Indeed, although male *Melissodes agilis* has been found to have eaten the most pollen early in the day, male *Nomia* and *Megachile rotundata* did not have time of day differences in pollen consumption (Dobson et al., *unpubl.data*). Thus, male bees theoretically have fewer temporal constraints. We also note that multiple smaller meals could result in less total pollen in a bee's gut at any given snapshot in time, resulting in an underestimation of total lifetime consumption.

Many other solitary bees share life-history traits with the nine species and five subgenera of economically significant apple-visiting *Andrena* studied here (Russo et al. 2015; Russo and Danforth 2017). Yet despite our initial supposition that *Andrena* could serve as a good proxy for insight into other solitary species, it is not clear the degree to which male pollen consumption is ultimately similar across bee genera. Taniguchi found ample pollen in the guts of Andrena and Colletes males (1956), but hardly any in *Osmia*, *Hylaeus, Anthophora*, and *Megachile.* In contrast, other work observed large numbers of *Chelostoma* and *Megachile* males had mostly full midguts (Dobson et al. *unpubl.data*), and contained diverse pollen (Käpylä 1978; Dobson et al. *unpubl. data*). The oil bee *Macropis fulvipes* has been directly observed eating *Lysimachia* pollen, but the quantity was not reported (Schäffler and Dötterl 2011). Finally, studies on other topics have recorded pollen consumption by solitary *Megachile rotundata* (Figueroa et al. 2021) and social *Bombus impatiens* (Fowler et al. 2020). Together, these findings show that *Andrena* cannot be assumed to represent solitary male bee pollen consumption, as different bee genera exhibit different patterns of pollen consumption.

Bees in our study could have been caught at any time in the several days the pan traps were out, meaning we cannot confidently rule out a relationship between day of the year and intraspecific pollen volumes. Future work should more systematically catch bees across their entire phenological and daily activity windows. Additionally, we note that the gut passage time of pollen digestion is not well established in wild solitary bees. It is not clear how much time may have passed since the pollen in the gut was consumed, or if digestion time varies based on life stage, sex, or time of day. In the future, we recommend separating out the segments of the gut, and separately quantifying the crop pollen in females, which in some species could contain pollen intended for regurgitation in the nest (sensu Cane et al. 2017; this phenomenon is not well-recorded in *Andrena* but see Rezkova et al. 2012 who interpret pollen mixed with nectar in the crop as being intended to help shape the pollen ball; but see Danforth 1990 where crop pollen of *Calliopsis persimilis* was found primarily on feeding "trips" after completing a cell, and thus interpreted as being for female nutrition, and similar interpretation of *Melissodes rustica* in Isenberg et al. 1997). By not quantifying regurgitation, we could be overestimating female pollen consumption and biasing the species richness estimate.

Ultimately, we found that male *Andrena* consume more pollen than previously suspected, although we confirm the expectation that males consume less than conspecific females in all but a few exceptional cases. Male solitary bees seem to be consistently foraging for and consuming pollen, yet implications remain unknown. It may be that adult male pollen consumption is beneficial for physiological maintenance, longevity, and/or fitness. Future research should explore whether male solitary bees consume pollen for its nutritional benefits for direct fitness-related traits such as sperm development and seminal fluid production, as well as indirect fitness-related traits such as longevity and vigor.

SUPPLEMENTARY INFORMATION

The online version contains supplementary material available at https://doi.org/10.1007/s13592-022-00951-4.

ACKNOWLEDGEMENTS

We would like to thank Steven Hoge for his invaluable help in the lab with pollen counting, Maria Van Dyke and Rachel Fordyce for support with *Andrena* taxonomy, Heidi Dobson for invaluable discussion, two anonymous reviewers for comments which improved the manuscript, and the growers and orchardists who allowed us collect these bees as part of the original study.

AUTHOR CONTRIBUTION

KRU conceptualized the study; KRU and EW conducted the literature review, developed the ideas, and completed lab work; KRU conducted the data analysis; EW and KRU wrote the manuscript; BND and SHM provided funding, logistical support, lab space, edits and comments. All authors read, edited, and approved the final version.

FUNDING

This work was funded by SARE Graduate Student Grant GNE18-188 and NSF Graduate Research Fellowship Grant No. 1650441, both awarded to KRU.

DATA AVAILABILITY

The dataset of the current study is available from the corresponding author on reasonable request.

CODE AVAILABILITY

The code used for this study is available from the corresponding author on reasonable request.

DECLARATIONS

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

Competing interests The authors declare no competing interests.

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