Intra-specific body size determines pollination effectiveness

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Abstract

Pollinators differ in morphological and behavioral traits. The effect of the resulting trait variation on pollination effectiveness at the level of different species has received considerable attention, while the effect of intra-specific trait variation at the population level is largely unexplored. We examined the impact of body size variation in the Red Mason bee *Osmia rufa* on the yield of oilseed rape in a caged field experiment. Crop yield was positively correlated to mean individual body size. Comparison with control plots showed that only large individuals increased yield to a level above pollinator-free variation. Small individuals, in contrast, even decreased yield compared to the variation within controls. Thus, the fitness of pollinator populations significantly affects pollination services, because adult body size is determined by the resource availability at the larval stage. Our results emphasize the need for complementing investigations on pollinator communities by analyses of the individual species involved. We conclude that only the availability of sufficient floral resources enables wild bee foragers to produce large, persistent offspring constituting effective pollinators for sustainable pollination services in the following season.

Zusammenfassung

Bestäuber unterscheiden sich in ihrer Morphologie und ihrem Verhalten. Die Auswirkungen der daraus resultierenden Variation in Eigenschaften für die Effektivität der Bestäubung sind auf der Gemeinschaftsebene gut untersucht. Die Auswirkungen von intra-spezifischer Variation auf der Ebene von Populationen sind hingegen größtenteils unerforscht. Wir haben den Einfluss von Körpergröße-Variation innerhalb der Roten Mauerbiene *Osmia rufa* auf den Ertrag von Raps in einem Käfig-Experiment untersucht. Der Ertrag war positiv mit der mittleren Körpergröße korreliert. Ein Vergleich mit Kontrollkäfigen ohne Bestäuber hat gezeigt, dass nur große Individuen den Ertrag über die Variation in der Kontrolle steigerten. Kleine Individuen dagegen haben den Ertrag im Vergleich zur Bestäuber-freien Kontrolle sogar gesenkt. Die Fitness innerhalb von Bestäuber-Populationen beeinflusst somit die Bestäuberleistung, da die Körpergröße der adulten Tiere von der Verfügbarkeit von Nahrungsressourcen während der Larvalphase bestimmt wird. Unsere Ergebnisse verdeutlichen die Notwendigkeit, bei Untersuchungen zu Bestäubergemeinschaften den Zustand der beteiligten Populationen mit zu berücksichtigen. Wir schlussfolgern, dass nur die Verfügbarkeit ausreichender Blütenressourcen es Wildbienen ermöglicht, große und ausdauernde Nachkommen für eine nachhaltige Bestäuberleistung in den folgenden Jahren zu produzieren.

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Introduction

Pollination is an important ecosystem process with economic and ecological relevance for arable crops and wild flowers (Klein et al. 2007; Ollerton, Winfree, & Tarrant 2011). Wild bees are generally considered the most important pollinator group in many ecosystems (Free 1993; LaSalle & Gauld 1993). Pollination efficiency differs among flower visitors (Sahli & Conner 2007), with larger species often being more effective (Kandori 2002). However, although body size also varies considerably within species (Goulson et al. 2002; Peat, Darvill, Ellis, & Goulson 2005), the effect of intra-specific trait variation on pollination efficiency at the population level remains largely unexplored. Some studies have shown intra-specific differences in foraging behavior related to body size for social bumblebees, a group known for considerable size variation in the worker class (Peat, Tucker, & Goulson 2005; Willmer & Finlayson 2014). Here, we examine the effect of individual body size of a solitary wild bee on yield in the mass-flowering crop oilseed rape.

Body size variation within wild bee species is predominantly determined by trophic and not by genetic factors (Tepedino, Thompson, & Torchio 1984; Couvillon & Dornhaus 2009). Large females provide more food to their offspring than smaller ones (Roulston & Cane 2009), thereby producing larger females in the following generation. This may have far-reaching ecological consequences, since larger individuals are more robust against habitat fragmentation, owing to the fact that individual body size is positively related to dispersal capacity (Warzecha, Diekötter, Wolters, & Jauker in press). Accordingly, the loss of flower resources and reduced availability of forage in agroecosystems increase the extinction risk at the community level (Müller et al. 2006; Memmot, Craze, Waser, & Price 2007; Goulson, Nicholls, Botías, & Rotheray 2015). At the same time, isolation of foraging habitats shifts body size distributions in local populations toward larger individuals, followed by a reduction in the number of plant species visited (Warzecha et al. in press). It is yet unknown whether the performance of individual pollinators within populations for specific plant species is similarly affected by body size.

Reduction in pollination service caused by intra-specific trait variability poses a considerable threat to both wild flowers (Biesmeijer et al. 2006) and an increasingly pollinator-dependent agriculture (Aizen, Garibaldi, Cunningham, & Klein 2008). Here, we were interested in whether intra-specific pollinator body size variation affects the pollination service provided to mass-flowering crops. We used oilseed rape (Brassica napus), one of the most common energy crops in the EU (van der Velde, Bouraoui, & Aloe 2009; FAO, 2015) to test pollination success of the Red Mason Bee Osmia rufa (L.), synonym O. bicornis, an efficient pollinator of this crop (Jauker, Bondarenko, Becker, & Steffan-Dewenter 2012). We hypothesize that larger individuals have a higher pollination efficiency and increase the yield parameters of oilseed rape.

Materials and methods

Experimental design

The study was carried out at the research station Weilburger Grenze of the Justus Liebig University Giessen, Germany. The experimental design was implemented on an approx. 1.5 ha winter-sown oilseed rape field (hybrid MAXIMUS PR44D06; Pioneer hi-bred Northern Europe division GmbH, Buxtehude, Germany) on allochthone Vega soil. Standard soil preparation and sowing was conducted on August 29 and 30, 2014. Field management included regular fertilizer application (calcium ammonium nitrate: 40 kg/ha on September 29, 2014, 90 kg/ha on March 18, 2015; boron: 2.0 l/ha on October 15, 2014; nitrogen: 63 kg/ha and sulphur: 72 kg/ha, both on February 2, 2015) and pest management (herbicides: Fuego Top, 2.0 l/ha, and Agil-S, 0.5 l/ha, on September 25, 2014; Cohort, 1.25 l/ha on March 19, 2015; insecticides: Bulldock, 0.3 l/ha on September 25, 2014; Trebon 30, 0.2 l/ha on March 19, 2015; fungicides: Ampera, 1.5 l/ha on October 15, 2014; Orius P, 1.0 l/ha on April 10, 2015).

The experimental design comprised 5×4 plots ($N = 20$, 148.5 m^2 total area) approx. 10 m from the northern edge of the field, established by mechanically removing oilseed rape plants from 1-m corridors and resulting in a plot area of 1.5×1.5 m each. Pollinator treatments were established in a pseudo latin square, including four closed control plots (no bees). All plots were caged with iron frames covered with fine mesh plastic gauze (cage length 1.5 m, width 1.5 m, height 2 m; cage area 2.25 m^2; mesh size c. 1 mm). With the exception of the four closed controls, plots were equipped with a trap nest consisting of approximately 150 internodes of Common Reed Phragmites australis (Cav.) in a plastic tube of 10.5 cm diameter on April 21, 2015 to stimulate nest building and foraging. Flowering at the field started on April 25, 2015.

Pollinator treatment

A total stock of 290 red mason bee cocoons (WAB-Mauerbienenzucht, Konstanz, Germany) was individually weighed (139 female, 151 male). Individuals were ranked according to weight, and sixteen weight categories were defined evenly along the gradient, separately for females and males. From each category, five females and two males closest to the median of the category were chosen for the experiment ($N = 80$ females and 32 males), i.e. seven individuals per cage. The 112 bees from the 16 body size categories were introduced into the flight cages by individually attaching open plastic tubes with the cocoons to the trap nests on May 2, 2015. Unhatched cocoons were manually opened on May 8, 2015 and dead individuals were replaced with manually opened ones from the same size category (20 females and 19 males), previously stored at 4 °C. The mean weights

Table 1. Distribution of mean cocoon bee weights among cages, separately for females and males and combined as *z*-scores (values relative to the mean of the whole population). Flowers per m^2 are the product of plant density per m^2 and the mean sum of pods and podless stalks per flower. Four control cages were not stocked with bees.

Ranked cage number	Mean weight females [mg]	Mean weight males [mg]	z-Scores [relative to mean]	Flowers m^{-2}
1	81.8 ± 1.2	47.6 ± 0.1	0.66 ± 0.06	5382
2	87.6 ± 0.9	51.6 ± 0.4	0.70 ± 0.07	6325
3	92.8 ± 0.5	56.5 ± 0.1	0.76 ± 0.05	3950
4	97.5 ± 1.6	63.4 ± 0.1	0.80 ± 0.04	3502
5	104.2 ± 0.5	67.5 ± 0.3	0.86 ± 0.04	4932
6	106.4 ± 0.4	72.8 ± 0.1	0.89 ± 0.02	4106
7	111.4 ± 1.0	75.8 ± 0.3	0.93 ± 0.03	6110
8	116.0 ± 0.3	82.5 ± 0.1	0.98 ± 0.01	6075
9	121.8 ± 0.9	88.2 ± 0.2	1.03 ± 0.01	8661
10	126.2 ± 0.9	92.3 ± 0.1	1.07 ± 0.01	7824
11	130.5 ± 0.9	97.1 ± 0.6	1.11 ± 0.02	6546
12	135.7 ± 0.9	102.8 ± 0.6	1.16 ± 0.03	5873
13	142.7 ± 0.7	107.1 ± 0.5	1.22 ± 0.02	5276
14	146.0 ± 0.7	112.3 ± 2.1	1.25 ± 0.05	6952
15	150.4 ± 2.9	118.9 ± 0.8	1.30 ± 0.05	11,492
16	167.1 ± 3.7	129.9 ± 12.6	1.45 ± 0.1	9028
Open control 1				10,482
Open control 2				4908
Open control 3				3873
Open control 4				5856

per cage are given in Table 1. Regular observations confirmed bee activity in all cages until the end of flowering on May 29, 2015. Cages were removed from the field on June 18, 2015.

For assessing the relationship between cocoon weight and adult body size, 13 females and 15 males from the remaining bee individuals spanning the respective weight gradient were manually extracted from the cocoon, frozen and pinned. For each specimen we measured the inter-tegular distance with a Keyence digital microscope at 50× magnification.

Yield components

Plants were harvested on July 4, 2015. First, all plants with contact to the cage mesh within 0.25 m from each edge of the plot were removed and discarded. In the remaining 1 m^2 plot, plant density was assessed and five plants were randomly chosen from the center and transferred to the laboratory ($N = 100$). For each plant, we counted undeveloped flower stalks and number of pods. Pods were manually opened and all seeds per plant were weighed and automatically counted (seed counter Contador, Pfeuffer, Kitzingen, Germany). Empty pods and plant residues were dried at 105 °C for 24 h and weighed for plant dry biomass. From the obtained data we assessed the following yield parameters: fruit set (relative number of flowers developing pods), seed set (mean number of seeds per pod), seed weight (calculated for 1000 seeds), and yield (seed weight per plant). We used the mean per plot for further analyses. During storage in an outdoor greenhouse, 21 plants were lost to squirrels (*Sciurus*

vulgaris). Thus, mean yield components were based on five plants for seven plots, on four plants for seven plots, and on three plants for four plots. Two plots were excluded from further analyses, because only two plants were left.

Data analysis

All statistical analyses were carried out using R, version 2.15.1 (R Development Core Team, 2012). The relationship between cocoon weight and adult body size (measured as inter-tegular distance: ITD) was analyzed using the lm.function. Normal distribution of variables was checked visually and homogeneity of variance by plotting fitted values vs. residuals of the model.

The effect of pollinator body size on yield components was assessed with linear models ($N = 14$). The explanatory variable was the mean pollinator weight per plot. We used *z*-scores, i.e. individual values in relation to the mean of females and males, respectively, because of differences in maximum and minimum body size between females and males. Dependent variables were the yield components fruit set, seed set, seed weight, and yield. Each yield component was analyzed separately. Intercorrelation of yield components, i.e. the dependency of yield on fruit set, seed set, and seed weight, was analyzed with a linear model using yield as the dependent variable.

Prior to analyses, collinearity of explanatory variables with confounding factors (plant density) was excluded. Normal distribution of dependent variables was determined visually

and significant models were tested for homogeneity of variance by plotting fitted values vs. residuals.

Results

Adult body size (ITD) was significantly and positively related to cocoon weight for females ($N = 13$, $F = 210.9$, $p < 0.001$) and males ($N = 15$, $F = 185.2$, $p < 0.001$). Males were lighter (and smaller) than females on average, but the slope was similar (Fig. 1).

Overall, 75 plants with approximately 475,000 seeds from 31,931 pods weighing 2.1 kg were harvested and analyzed. In the four reference closed control cages with no pollinators, fruit set averaged at 0.59 ± 0.03 standard deviation, seed set at 14.2 ± 1.2 seeds per pod, seed weight at 4.7 ± 0.3 g per 1000 seeds, and yield at 27.8 ± 3.6 g per plant.

Mean pollinator body size significantly affected yield ($F_{1,12} = 7.49$, $p = 0.018$), without impacting any of the other parameters (fruitset $F_{1,12} = 0.12$, $p = 0.733$; seedset $F_{1,12} = 0.53$, $p = 0.481$, seed weight $F_{1,12} = 0.07$, $p = 0.802$). Plants exposed to small bee individuals achieved only half of the yield compared to those pollinated by large individuals (Fig. 2). Plotted against the mean yield and 95% confidence interval range of the four closed control cages with no pollinators, only large bees increased yield above levels of pollinator-free controls. Exposure to small bees, in contrast, resulted in yields below the levels of pollinator-free controls (Fig. 2). No significant relationship between yield and the remaining yield components seed set, fruit set, and seed weight could be established ($F_{1,12} = 1.09$, $p = 0.316$), even after subsequently removing the least significant predictors. Plotting yield against the standardized ranges of the yield components suggests positive trends for seed set and fruit set, and a negative trend for seed weight (Appendix A).
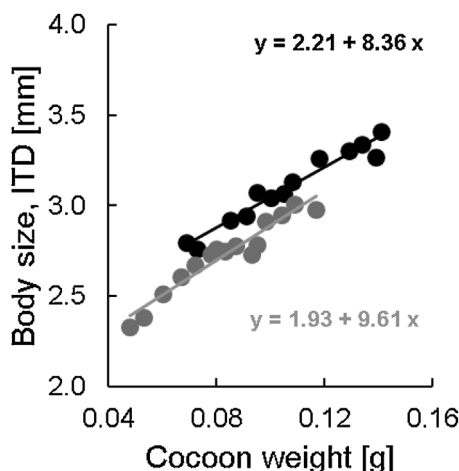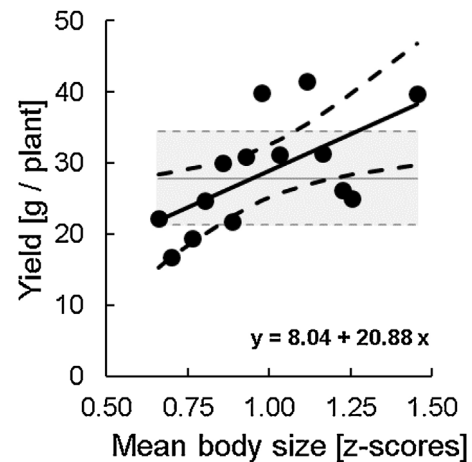
Fig. 2. Relation between the mean body size (five females and two males per treatment) of the Red Mason bee *Osmia rufa*, expressed as *z*-scores of the cocoon weight, and the mean yield of rape plants expressed as total seed weight, including best-fit equation. The gray shaded area covers the 95% confidence interval (dashed gray lines) associated with the mean yield of closed control cages with no pollinators (solid gray line).

y = 8.04 + 20.88 x

Discussion

We investigated the influence of intra-specific body size in a solitary bee species on pollination effectiveness. Our results show that yield in oilseed rape doubles with an increase of mean body size of *Osmia rufa*. No significant relationship between yield components and neither pollinator body size nor yield could be established. Thus, benefits of pollinator body size to oilseed yield seem to be based on additive effects on mainly seed set and fruit set with little compensatory effects on seed weight (c.f. Free & Nuttall 1968). However, only the largest individuals exceeded yields obtained in a closed control with no pollinators.

In 2013, approx. 26 million tons of oilseed rape were harvested in the EU (FAO 2015). The pollinator contribution to yield can vary between 11 and 45% for oilseed rape (Sabbahi, Oliveira, & Marceau 2005; Lindström, Herbertsson, Rundlöf, Smith & Bommarco in press). Here, we show that within a single pollinator species, small individuals (66% of the mean body size) are only half as effective as large individuals (145% of the mean body size). Individual body size therefore seems to be similarly important to body size differences among species (Kandori 2002). Considering that body size variation of wild bee species is primarily determined by the nutritional status of the previous generation (Tepedino et al. 1984; Couvillon & Dornhaus 2009), improving the availability of flower resources to stimulate the production of larger offspring (Radmacher & Strohm 2010) may thus be a promising tool for increasing yields of pollinator-dependent crops.

The substantial positive effect of pollinator body size on yield emphasizes the pollination benefits also for oilseed hybrids, often regarded to be little affected by pollination

y = 2.21 + 8.36 x

y = 1.93 + 9.61 x

Fig. 1. Relation between cocoon weight of the Red Mason bee *Osmia rufa* and the body size as adults, measured as inter-tegular distance (ITD), including best-fit equation. Black: females ($N = 13$), gray: males ($N = 15$).

(Hudenwenz, Pufal, Bögeholz, & Klein 2014; Lindström et al. in press). At the examined pollinator density, however, only the largest individuals clearly elevated yields above control levels without pollinators. Remarkably, but less prominently, yield in cages with small bee individuals fell below the control yield levels. Pollination efficiency is mainly based on the amount of pollen deposited on a receptive stigma in relation to the pollen uptake of a pollinator (Inouye, Gill, Dudash, & Fenster 1994). It has been shown before that flower visitation per se is not directly related to pollination success, because – often subtle – costs with increased flower visitation (e.g. flower damage or transfer of poor quality pollen) partly offset benefits (Morris, Vásquez, & Chacoff 2010). Thus, we speculate that body size in relation to oilseed flower size is unfavorable for small individuals of *O. rufa* with regard to the amount and position of pollen on the insect (Tepedino, Sipes, & Griswold 1999) and the handling time or mode (Stout 2000; Vivarelli, Petanidou, Nielsen, & Cristofolini 2011). Under field conditions, a relatively low share of high-efficiency pollinators within pollinator communities offsets negative plant fitness effects of low-efficiency pollinators (Lau & Galloway 2004). Detrimental effects of small body size on pollination effectiveness within populations may similarly be suppressed under normal size distributions. It has recently been shown, however, that habitat fragmentation may shift pollinator body size distributions toward a larger share of smaller individuals (Warzecha et al. in press). Generally, future studies will have to show the extent to which pollination efficiency measured within the cages was modulated by the bee density chosen for this experiment (e.g. the low effect of medium-sized individuals).

We have shown that the intra-specific size variability of bee populations can modulate pollination effectiveness. This carries a great potential for managing ecosystem services, because mass-flowering crops provide foragers with ample floral rewards for the production of large, persistent offspring constituting effective pollinators in the next generation (Bosch & Kemp 2004). The efficacy of this ecological feedback, however, depends on the phenological match between pollinator species and crop (Jauker, Peter, Wolters, & Diekötter 2012; Diekötter, Peter, Jauker, Wolters, & Jauker 2014) and needs to be supported by temporally complementary flower resources (Holzschuh, Dormann, Tscharntke, & Steffan-Dewenter 2012). This need becomes more pressing when considering that poor pollinators, small individuals in our case, fail to achieve maximum yield levels expected under natural variation.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.baae.2016.07.004.

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