



# Relevance of diet diversification in the coexistence between *Orius laevigatus* and *Amblyseius swirskii*: prey switching and intraguild predation

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Received: 28 September 2023 / Revised: 12 February 2024 / Accepted: 14 February 2024

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## Abstract

Omnivores obtain resources from more than one trophic level, choosing food based on quantity and quality. They usually engage in intraguild predation (IGP) when prey is scarce. *Orius laevigatus* is an example of omnivore that becomes superior predator of the predatory mite *Amblyseius swirskii* when released in a combined system under low levels of the preferred prey, the thrips *Frankliniella occidentalis*. Here, we test two genetically enhanced *O. laevigatus* strains for bigger size and better fitness feeding on pollen (BIG30 and 2POL-11, respectively), hence with a wider dietary diversification, to elucidate the potential effects on prey preference and IGP on the predatory mite, in comparison with a commercial population of *O. laevigatus*. To do that, predation rates were registered on adult phytoseiids solely or in a choice situation at different availability ratios of adult thrips under laboratory conditions. The effect of pollen as supplemental food on IGP and prey preference was examined, too. We found that our two enhanced lines killed up to 9% less predatory mites and fed preferably on adult thrips, compared to the commercial population. While BIG30 showed a significantly higher total predation rate, killing up to 150% more adult thrips, 2POL-11 is defined as an efficient user of resources, switching between different prey and pollen showing low IGP. Pollen supplementation had a significant effect on reducing IGP, but only for 2POL-11 the influence on prey preference was significant. The theory of intraguild predation and the impact of prey switching on food webs and biological control strategies are also discussed.

**Keywords** Predation capacity · Body size · Omnivory · Selective breeding · Genetic improvement · Prey preference · Hemiptera · Anthocoridae

## Key message

- Omnivores, such as *Orius laevigatus*, select food from multiple trophic levels.
- Intraguild predation is common among *O. laevigatus* and *A. swirskii*, especially when prey is scarce.

- Tested intraguild predation (IGP) in two enhanced strains of *O. laevigatus*, with and without pollen.
- The enhanced lines killed less predatory mites and fed preferably on adult thrips.
- Pollen supplementation reduced IGP, especially on the strain selected for pollen tolerance.

## Introduction

Omnivory is a feeding strategy that confers *Orius laevigatus* (Hemiptera: Anthocoridae) a differential advantage over competing predators, since it allows this insect to remain longer in the crop feeding on alternative food resources, preventing a rapid subsequent build-up of pest populations (Coll 1998; Eubanks and Denno 2000; van Rijn 2002). However, when pest levels decline and omnivorous predators that feed

Communicated by Nuria Agustí.

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on plant resources available in the crop, such as pollen or nectar, are expected to express their phytophagy, they rather tend to intensify some competitive interactions which may be detrimental to biological control, attacking and consuming conspecifics (cannibalism) or other predators (intraguild predation, IGP). The latter situation is particularly true for a combined system widely used in the biological control of the key pests of greenhouse sweet pepper: the western flower thrips, *Frankliniella occidentalis* (Thysanoptera: Thripidae), and the greenhouse whitefly, *Bemisia tabaci* (Hemiptera: Aleyrodidae). Such system consists of *O. laevigatus* itself and the predatory mite *Amblyseius swirskii* (Acari: Phytoseiidae) (Chambers et al. 1993; Ramakers 1993; Brødsgaard 2004; Shipp and Ramakers 2004; Chow et al. 2008; Weintraub et al. 2011; Bouagga et al. 2018). Regarding western flower thrips, *O. laevigatus* is able to feed on both larvae and adults, while *A. swirskii* mainly kills eggs and first instar larvae of this pest (Wimmer et al. 2008; Nguyen et al. 2019), although it is more effective than other commercially available phytoseiid mites for the control of *F. occidentalis* on cucumber (Messelink et al. 2006), sweet pepper (Calvo et al. 2015) or cut rose (Pijnakker and Ramakers 2008). Some laboratory studies corroborated the compatibility between both predators, stating that intraguild predation not only does not harm but may even benefit biological control (Wittmann and Leather 1997; Weintraub et al. 2011). If *O. laevigatus* does not exhibit a preference for *A. swirskii*, the coexistence of both predators is likely to positively impact *O. laevigatus* ability to prey on thrips. Consequently, employing both predators can enhance thrips control, even if *A. swirskii*'s effectiveness is somewhat diminished. Additionally, in situations where thrips prey is scarce, *O. laevigatus* can resort to preying on *A. swirskii*, ensuring the survival of *O. laevigatus*. On the other hand, others reported a clear negative effect of such coexistence (Magalhães et al. 2004; Chow et al. 2010; Buitenhuis et al. 2015), supported by the status of *O. laevigatus* as a top predator or intraguild predator (IG predator) on *A. swirskii*, which in turn performs as an intermediate predator or intraguild prey (IG prey). Then, at low prey density, *A. swirskii* suffers both predation and competition from *O. laevigatus*, whereas the latter is only affected by phytoseiid competition when it shares the younger stages of thrips as prey. That results in a clear trade-off in coexistence and hence in the effectiveness of biological control of this pest (Rosenheim et al. 1995; Rosenheim 1998; Symondson et al. 2002; Janssen et al. 2007). Therefore, it is probably inappropriate to treat true omnivory and IGP as two separate ecological phenomena, as has been done in the past, since in many cases both interactions are expressions of a single underlying phenomenon of predators with a diversified diet (Shakya et al. 2009).

Still, Weintraub et al. (2011) proved that simultaneous release of *A. swirskii* and *O. laevigatus* is able to provide

similar levels of thrips control with lower anthocorid release ratios when compared to releasing only anthocorids. In fact, this combined release strategy is still recommended today and is well implemented in integrated control programs for greenhouse sweet pepper, especially due to the control of whiteflies, in order to minimize virus transmission (Calvo et al. 2012). Moreover, there is clear evidence that a non-prey food such as pollen manages to mitigate IGP as well as cannibalism (Leon-Beck and Coll 2007; Lundgren 2009; Calabuig et al. 2018; Marcossi et al. 2020), improving the suppression of pest populations by reinforcing predators and at the same time promoting pest co-suppression by the IG predator and the IG prey, and even allowing the total elimination of the shared resource, in this case thrips (Daugherty et al. 2007; Delisle et al. 2015; Ghasemzadeh et al. 2017). In this context, the results of Calabuig et al. (2018) suggest that *Typha angustifolia* L. (Typhaceae: Poales) (Nutrimite) pollen is suitable to blunt these negative interactions between generalist predatory mites such as *Euseius stipulatus* and *Iphiseius degenerans* (Acari: Phytoseiidae) both among themselves and on *Aphidoletes* sp. (Diptera, Cecidomyiidae) eggs. Similarly, Onzo et al. (2005) found that the addition of abundant levels of corn pollen increased the survival and reproduction of two phytoseiid mites, *Typhlodromalus manihoti* and *Euseius fustis* (Acari: Phytoseiidae), and reduced IGP between them to minimal levels. Also, they found a positive effect of corn pollen not only on interactions between the two predators, but also on suppressing prey population densities in greenhouse experiments.

The degree of trophic specialization and relative body size are two factors strongly impacting the frequency and directions of IGP (Polis et al. 1989). Not surprisingly, IGP is often preferentially directed toward the predator's closest potential competitors (i.e., those with the greatest resource overlap), and it is worth noting that both predators in the present system, *A. swirskii* and *O. laevigatus*, share resources such as pollen or the youngest stages of thrips. Either because of a niche overlap or as a result of direct selection to feed on these resources, interactions between the two predators are typically frequent. In this context, Daugherty et al. (2007) modeled a very limited coexistence between the two predators if the IG predator were supplemented with a plant-based food such as pollen, arguing that such feeding tends to exclude both the IG prey and the herbivore. Maybe for this reason or perhaps because of spatial dynamics, Shakya et al. (2009) evidenced how IGP between *O. laevigatus* (IG predator) and *Neoseiulus cucumeris* (Oudemans) (IG prey) grew in intensity in the presence of pollen when switching from experiments in simplified settings to whole plants, with both predators consuming significantly more thrips in the absence of pollen than in the presence of it. Given this, it becomes even more necessary to conduct an extensive intraguild predation study with an artificially

selected strain of *O. laevigatus* selected for better fitness feeding on pollen (Mendoza et al. 2020a) to evaluate coexistence with *A. swirskii* under conditions of prey scarcity, given its enhanced reproductive performance when feeding exclusively on pollen.

On the other hand, most of IGP interactions occur in systems with size-structured populations by generalist predators that are usually larger than their intraguild prey (Polis et al. 1989). In this context, a larger body size predator such as those from the improved line BIG30, obtained through a selective breeding program for larger size (Mendoza et al. 2020b), presents, on the one hand, a significantly higher predatory capacity (Mendoza et al. 2022), which at the same time could result in a more intense IGP on *A. swirskii*, given the size difference between both predators (Woodward and Hildrew 2002). On the other hand, precisely because of its high voracity, it may undergo a diversification in its diet, resulting in a higher IGP (Woodward and Hildrew 2002). At the same time, a hungry consumer can move more actively and come into contact with IG predators more frequently (Polis et al. 1989). For all these reasons, it would be interesting to test a model of interaction between both predators as well as in a tritrophic system that includes the adult thrips as an extraguild prey, not preyed by the phytoseiid, which would also allow us to evaluate the preference of BIG30 individuals for a larger prey in this case, given the higher nutritional requirement of the enhanced strain to reach a larger size (Mendoza et al. 2022). In the same line, it would also be very interesting to assess any potential variation in BIG30's omnivory as a result of the breeding process, testing the effect of pollen addition on predatory ability and/or the preference for predatory mites or flower thrips.

To test these hypothesis two experiments were conducted. In non-prey choice bioassays, the IGP on *A. swirskii* of two artificially selected *O. laevigatus* strains, 2POL-11 selected for better fitness on pollen (Mendoza et al. 2020a) and BIG30 selected for larger body size (Mendoza et al. 2020b) was compared with that of a commercial population. In a second experiment, prey switching between *F. occidentalis* and *A. swirskii* was also compared among the same *O. laevigatus* strains in the presence or absence of pollen.

## Materials and methods

### Insects and mites rearing

The Biocontrol Selection Lab of the Universidad Politécnica de Cartagena has developed selective breeding programs (Bielza et al. 2020) for several key traits for the field performance of *O. laevigatus*, such as insecticide resistance (Balanza et al. 2019, 2021a,b, 2022), larger body size (Mendoza et al. 2020b) and better fitness feeding on pollen (Mendoza

et al. 2020a). The enhanced *O. laevigatus* populations, BIG30 selected for larger body size (Mendoza et al. 2020b) and 2POL-11 selected for better fitness on pollen (Mendoza et al. 2020a), were used in this study. A commercial population from Agrobio S. L. (Almería, Spain, ORIcontrol<sup>®</sup>, hereafter Agrobio) was used as baseline or control. All predator populations were maintained feeding on *Ephesia kuehniella* eggs under controlled conditions at  $26 \pm 1$  °C,  $70 \pm 10\%$  RH and 16:8 L:D photoperiod.

Commercially available *A. swirskii* population (SWIRScontrol<sup>®</sup>) was also provided by Agrobio for the IGP bioassays, both for the no-choice and the prey switching bioassays. To conduct our prey switching bioassays, synchronized young *F. occidentalis* adults (15–17 days old) were supplied from a rearing system on green bean pods established at the Universidad Politécnica de Cartagena, comprising several field populations originally collected from organic production greenhouses in southeastern Spain between 2009 and 2010 and then mixed as explained in Guillen et al. (2014).

### Non-prey choice bioassays

To evaluate the intraguild predation (IGP) of *O. laevigatus* on *A. swirskii*, 5-mL plastic vials containing 3, 5, 10, and 30 two-day-old adult mites were prepared. Each vial included a 30×5 mm segment of pepper leaf, covered by a carefully punctured lid (3–4 holes of <0.5 mm). After 24 h of exposing adult *O. laevigatus* to the mites and a subsequent 24-h period of starvation, a single *O. laevigatus* female aged between 3 and 7 days was introduced into each vial. Twenty replicates were conducted for each *O. laevigatus* population (BIG30, 2POL-11, and Agrobio) and dose, with half of the replicates supplemented with powdered commercial dehydrated honeybee pollen (Hijas del Sol<sup>®</sup>, hereafter referred to as pollen), and the other half without it. In these experiments, the variability between male and female mites was minimized by selecting adults of comparable size approximately 24 h after being provided by the commercial source. A control dose was also assessed to examine the survival of phytoseiids in the absence of the predator, both with and without pollen. After 24 h, the count of dead intraguild prey was recorded, and the width of the pronotum of female *O. laevigatus* was measured (after freezing) under a binocular microscope with a micrometer at 50× magnification.

### Prey switching bioassays

A prerequisite for the study of prey alternation behavior by a predator is the avoidance of large numbers of each prey type. Having determined the appropriate range of prey densities to use in alternation studies based on the assessment of predation on *F. occidentalis* and *A. swirskii*, prey switching was

evaluated by offering females of the *O. laevigatus* populations tested, different proportions of thrips and phytoseiid. For each *O. laevigatus* population examined, we used a similar protocol to that followed in the no-choice experiments and exposed individual *O. laevigatus* females for 24 h to the following prey ratios: 5 *F. occidentalis* and 15 *A. swirskii* (1:3 ratio), 10 *F. occidentalis* and 10 *A. swirskii* (1:1 ratio), 15 *F. occidentalis* and 5 *A. swirskii* (3:1 ratio), with and without pollen supplementation. First, the required number of adult thrips and then adult mites were transferred into each plastic vial together with a rectangular cut of pepper leaf inside. Half of the vials were sprinkled with pollen. A female *Orius* was then released into each vial, and a perforated lid was placed on top to prevent the arthropods from escaping. Twenty-four hours later, the number of dead prey and IGP prey in each vial was checked and the *O. laevigatus* were frozen for measurement at 50x. Ten replicates per prey ratio and per supplementation treatment were completed for Agrobio, BIG30 and 2POL-11 ( $n = 180$  *O. laevigatus*). In order to assess natural mortality, control consisted of the same three series of prey ratios and both supplementation treatments, but without female *Orius* (ten replicates each).

## Statistical analysis

For the prey alternation bioassays, the null or “no-switch” model for a system consisting of two prey species (Murdoch 1969) was followed:

$$P_1 = \frac{C \cdot F_1}{1 - F_1 + C \cdot F_1} \quad (1)$$

where  $F_1$  is the proportion of prey species 1 (in our case, *F. occidentalis*) in the environment,  $P_1$  is the proportion of prey species 1 among all prey consumed by the predator, and  $C$  is a measure of the predator’s preference for prey species 1, which is given by:

$$C = \frac{N_1/N_2}{H_1/H_2} \quad (2)$$

where  $H_1$  and  $H_2$  are, respectively, the number of prey of species 1 (*F. occidentalis*) and 2 (*A. swirskii*) present in the environment (offered prey), and  $N_1$  and  $N_2$  are the quantities actually consumed (attacked prey) by *O. laevigatus* females. If no prey switching occurs,  $C$  is constant and can be predicted for any  $H_1/H_2$  ratio. If predator preference is not constant, but varies with prey availability or encounter rates,  $C$  is expected to increase as  $H_1/H_2$  decreases. Therefore, if alternation occurs, the observed proportion of *F. occidentalis* among all prey killed will be higher than expected when that species is more abundant and correspondingly lower when it is not as common.

$C$  should be estimated when both prey classes are equally available,  $H_1 = H_2$ . Thus, for each replicate of the 1:1 test set, we estimated a value of  $P_1$  by substituting  $C$  into Eq. (1). These estimates were used to calculate the expected number of *F. occidentalis* adults among all prey killed in each replication of the 5:15 and 15:5 trial sets. Following the statistical procedure described in Chow and Mackauer (1991),  $P_1$  values were calculated and observed numbers of *F. occidentalis* killed were compared with numbers predicted from the null or no-switch model.

Data on predation rates of the three populations tested at different densities of adult thrips were extracted from no-choice trials carried out and discussed by Mendoza et al. (2022) to compare them with the results of our null or no-switch model.

Linear regression tests were conducted between the proportion of dead mites and pronotum width from *O. laevigatus* to determine the influence of female size on IGP. Counts and proportions were tested for normality using the Shapiro–Wilk test as well as homoscedasticity by a Levene’s test. Since the assumptions of normality and homogeneity were not met, Wilcoxon signed-rank tests were used to compare the observed numbers of dead thrips with the numbers predicted by the no-switch model. Differences in predation rates were subjected to a multivariate analysis (ANOVA) with *O. laevigatus* population, pollen treatment and predatory mite density as independent variables. Counts and proportions of all populations and treatments were transformed to their square root and arcsine values, respectively, to meet the assumptions of normality and equality of variances. Differences between populations in pronotum width were determined using one-factor ANOVA. Finally, ANOVA was also performed to compare the number of dead prey recovered from the controls. Tukey’s multiple comparisons test (HSD) (Sokal and Rohlf 1995) for  $p < 0.05$  was used for all analyses, solving for pairwise differences between means. Dead females of *O. laevigatus* were excluded from the analysis.

## Results

### Non-prey choice bioassays

Mite density showed a significant influence on the predation rate of *O. laevigatus* females under laboratory conditions (multifactorial ANOVA:  $F_{3, 239} = 29.62$ ,  $p < 0.001$ ). In fact, predation rate increased with the number of mites offered to each female regardless of the population tested (density-population:  $F_{6, 239} = 1.79$ ,  $p = 0.102$ ) and the availability of pollen as a food supplement (density-pollen interaction:  $F_{3, 239} = 2.02$ ,  $p = 0.111$ ) (Table 1). On the other hand, the use of pollen as a supplement also had a significant effect on IGP ( $F_{1, 239} = 16.60$ ,  $p < 0.001$ ), which was lower in the

**Table 1** Number of prey consumed (mean  $\pm$  standard error) per *O. laevigatus* female when feeding on various densities of *A. swirskii*, with or without pollen supplementation

Prey density	No. of mites consumed/♀ 24 h (mean $\pm$ standard error)					
	Without pollen			With pollen		
	Agrobio	2POL-11	BIG30	Agrobio	2POL-11	BIG30
3	2.5 $\pm$ 0.2 <sup>Ba</sup>	2.3 $\pm$ 0.2 <sup>Ba</sup>	2.8 $\pm$ 0.1 <sup>Ca</sup>	2.4 $\pm$ 0.2 <sup>Ba</sup>	1.1 $\pm$ 0.2 <sup>Aa</sup>	2.5 $\pm$ 0.2 <sup>Ba</sup>
5	4.0 $\pm$ 0.3 <sup>Cb</sup>	2.7 $\pm$ 0.3 <sup>Ba</sup>	4.2 $\pm$ 0.2 <sup>Cb</sup>	2.9 $\pm$ 0.4 <sup>Ba</sup>	1.7 $\pm$ 0.3 <sup>Ab</sup>	4.0 $\pm$ 0.3 <sup>Cb</sup>
10	6.6 $\pm$ 0.4 <sup>Cc</sup>	4.2 $\pm$ 0.6 <sup>Bb</sup>	7.1 $\pm$ 0.3 <sup>Cc</sup>	4.5 $\pm$ 0.5 <sup>Bb</sup>	2.5 $\pm$ 0.5 <sup>Ab</sup>	6.6 $\pm$ 0.4 <sup>Cc</sup>
30	15.9 $\pm$ 0.9 <sup>Cd</sup>	12.4 $\pm$ 0.8 <sup>Bc</sup>	16.9 $\pm$ 0.5 <sup>Cd</sup>	13.0 $\pm$ 1.0 <sup>Bc</sup>	7.4 $\pm$ 0.5 <sup>Ac</sup>	15.9 $\pm$ 0.9 <sup>Cd</sup>

Values followed by different lowercase letter in the same column and different uppercase letter in the same row are significantly different (Tukey's test,  $p < 0.05$ )

presence of pollen than in the absence of it. Although such decrease was observed for the three bioassayed populations (population-pollen interaction:  $F_{2, 239} = 2.05$ ,  $p = 0.131$ ), it was especially relevant in the pollen-tolerant population, 2POL-11, where a decrease of up to 43% in IGP was recorded when pollen was supplied together with the highest dose of mites (30 individuals per female) (Table 1). However, the main result of our non-prey choice bioassays is the difference in IGP rate as a function of the population tested ( $F_{2, 239} = 38.40$ ,  $p < 0.001$ ). Thus, regardless of phytoseiid density, while females of the commercial population (Agrobio) prey on 53% of the mites presented to them, those of the enhanced population for larger body size (BIG30) exceed 70% predation, and in contrast, females of the population adapted to prey scarcity (2POL-11) do not reach 40%. These results are consistent with the difference in mean size recorded for females from each of these populations (one-factor ANOVA:  $F_{2, 239} = 105.77$ ,  $p < 0.001$ ), with a mean pronotum width of 0.747 (0.742–0.753) mm for 2POL-11, 0.777 (0.771–0.782) for Agrobio and 0.829 (0.824–0.835) for BIG30. Accordingly, and supported by the obtained correlation coefficient (0.608), it could be determined that IGP is relatively dependent on predator size ( $R^2 = 36.9\%$ ,  $p < 0.001$ ).

On the other hand, mortality of *A. swirskii* was very low in the controls. Furthermore, the mean number of dead mites recovered from the controls (without pollen: mean  $\pm$  standard error = 0.63  $\pm$  0.15, with pollen: 0.53  $\pm$  0.18,  $n = 10$ ) was, on average, 11–12% of those observed in the treatments with one *Orius* female and 10 mites per replicate. It can be asserted, therefore, that phytoseiid mortality is almost entirely due to predation by *O. laevigatus* females.

### Prey switching bioassays

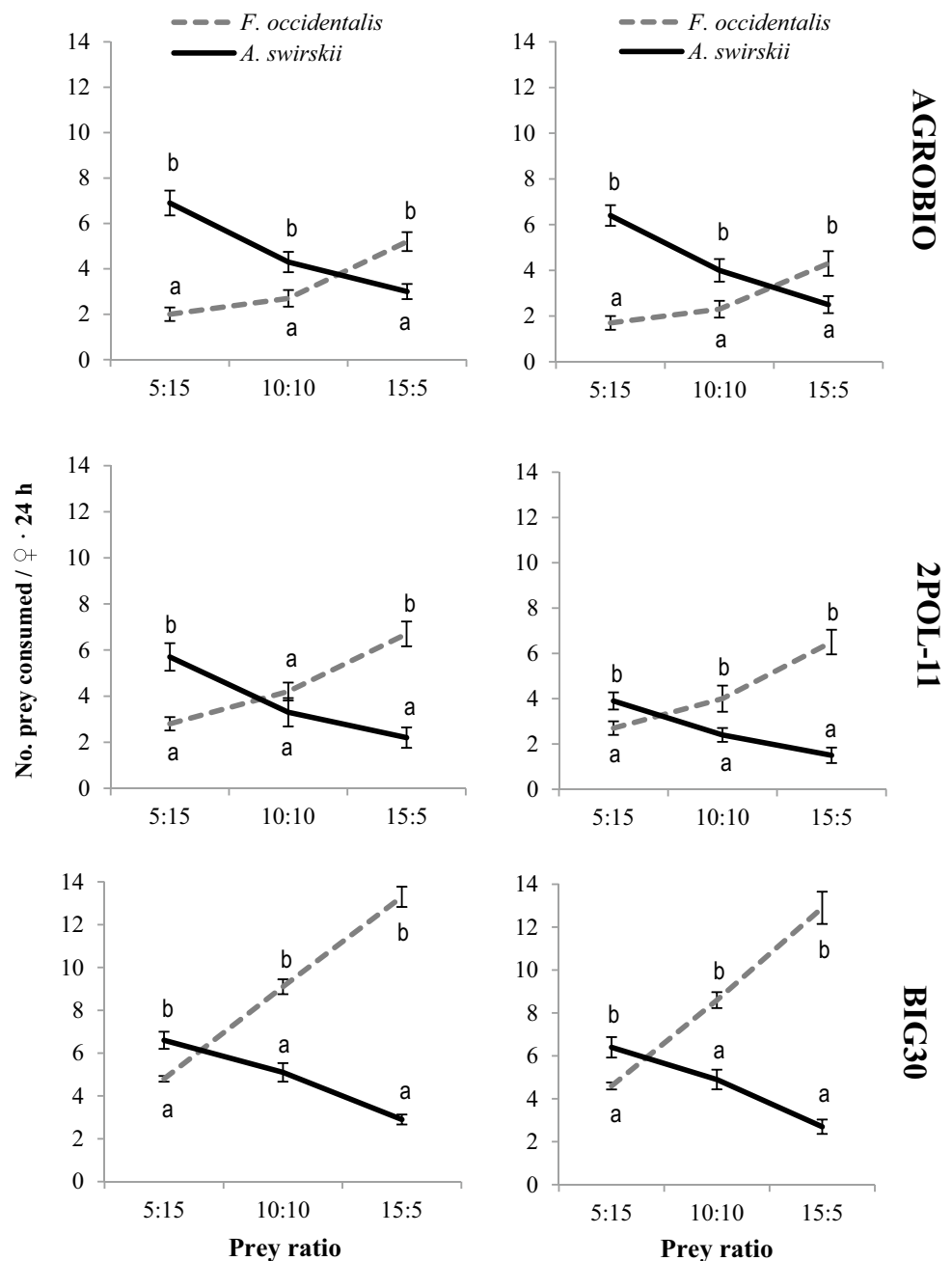
*O. laevigatus* females of the three populations tested tended to prefer the prey shown in higher proportion (Fig. 1). However, when the ratio of both prey was 10:10, the Agrobio population showed a clear preference for *A. swirskii* over *F. occidentalis* adults, but not in the case of the enhanced populations 2POL-11 and BIG30.

In fact, when *F. occidentalis* adults were offered to Agrobio females as the predominant prey species (15:5 ratio), they preyed on 47–52% fewer thrips than expected based on the null or non-switching prey model (Table 2), demonstrating a greater preference for the phytoseiid mite. In contrast, for the enhanced *O. laevigatus* genetic lines, a very different switching pattern was observed between the two prey species (Fig. 1).

In the case of the population tolerant to non-prey feeding, 2POL-11, a clear pattern of alternation between both types of prey than in Agrobio was observed in the absence of pollen, as no significant differences were observed in predation on both when they were equally supplied, clearly tending toward the more abundant species in each case (Fig. 1). More importantly, a kind of shift from intraguild to extraguild predation in 2POL-11 (compared to what occurred in Agrobio) took place after supplementing the diet with pollen. Indeed, although the addition of pollen did not result in an increase in the predation rate on adult thrips compared to what was expected according to the null model (Table 2), the counts of thrips and phytoseiids attacked in a 10:10 ratio were significantly deviated toward the pest. This significant effect of pollen addition on IGP in this population ( $F_{1, 179} = 6.33$ ,  $p < 0.05$ ) is reinforced by a reduction by 9% in the predation rate on phytoseiid mites when pollen-tolerant females are provided with pollen. Besides, the proportion of phytoseiid mites killed relative to total prey was significantly lower among pollen-tolerant females than that of the other two populations tested (multivariate ANOVA:  $F_{2, 179} = 15.05$ ,  $p < 0.001$ ), with 30% of mites attacked by these females compared to 45–46% of mites attacked by those of Agrobio and BIG30.

In the case of the size-enhanced population, BIG30, there was a clear preference of *Orius* females for extraguild prey both in the presence and absence of pollen as supplementary food (Fig. 1). However, contrary to what occurred in the pollen-tolerant strain with pollen, the superior preference for thrips was not due to a decrease in the intensity of the IGP compared to that of the commercial population, but rather to a significant increase in the predation on adult thrips ( $F_{2, 177} = 77.71$ ,  $p < 0.001$ ). On the one hand, its

**Fig. 1** Number of adults (mean  $\pm$  standard error) of *Frankliniella occidentalis* (FO, dashed lines) and *A. swirskii* (AS, solid lines) consumed by a single female *O. laevigatus* of commercial (Agrobio, top) and selected (2POL-11, center; BIG30, bottom) lines in a choice situation with different prey ratios (FO: AS), with (right) or without (left) pollen. For each prey ratio, different letters indicate significant differences (Wilcoxon signed-rank test,  $p < 0.05$ )



females preyed two to three times more adult thrips than the other two populations tested when both prey were in the same proportion. Moreover, for this population alone, a level of predation on adult thrips similar to that expected under the null or no-switch model was achieved at the highest pest density (Table 2). Finally, even when thrips were less abundant in the combined system (ratio 5:15), BIG30 females preyed 142–150% more than expected according to the model proposed by Murdoch (1969). In short, the total predatory ability of BIG30 females, with a significantly larger pronotum width and thus larger than those of Agrobio or 2POL-11 ( $F_{2, 177} = 107.85, p < 0.001$ ), is also significantly

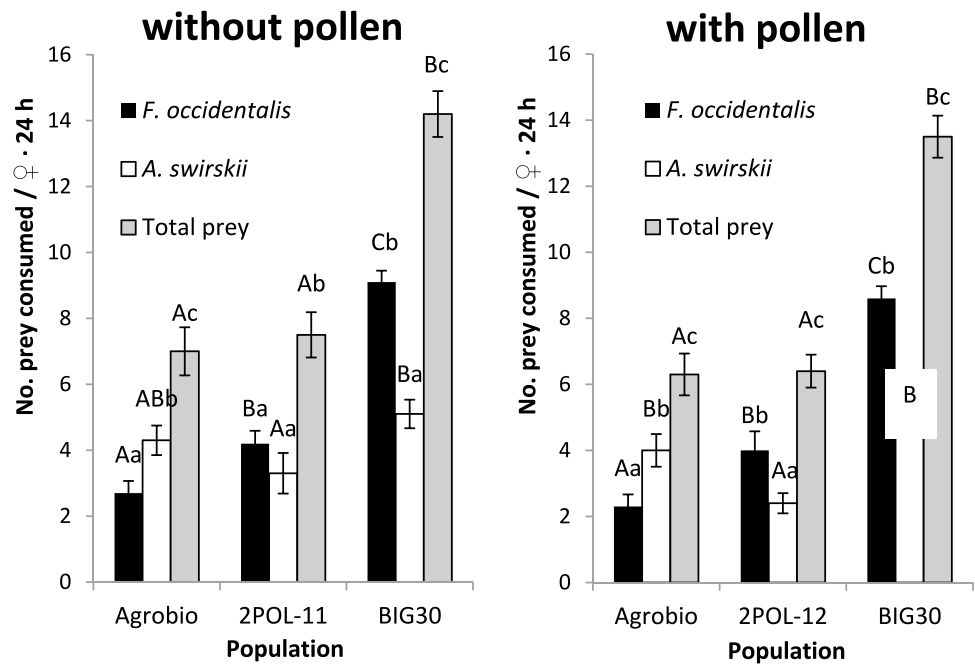
the highest of those recorded in our trials (multivariate ANOVA:  $F_{2, 179} = 128.03, p < 0.001$ ) (Fig. 2), being in any case lower with pollen as a food supplement ( $F_{1, 179} = 8.57, p < 0.01$ ). Thus, in a situation of choice between an IG prey and the adult of their focal prey, females of the larger population consumed almost twice as much prey as those of the other two populations tested (13.7 vs. 7.6–7.7 prey per day). In addition, the proportion of adult thrips in this total consumption is significantly higher in BIG30 (44%) than in Agrobio (15%) or 2POL-11 (22%) (multivariate ANOVA:  $F_{2, 179} = 77.86, p < 0.001$ ), thus demonstrating the greater preference of this enhanced strain for adult flower thrips.

**Table 2** Observed and expected number of consumed *F. occidentalis* (FO) adults recovered after 24 h of contact with isolated *O. laevigatus* females, in different proportions of *F. occidentalis* and *A. swirskii* (AS), with or without pollen supplementation

	Population	No. of adults of <i>F. occidentalis</i> consumed/♀ 24 h	df			Probability <sup>a</sup>	
			(mean ± standard error)	Prey ratio (FO:AS)	Observed		Expected
Without pollen	Agrobio <i>n</i> = 10	5:15	2.00 ± 0.30	0.90 ± 0.08	18.0	18	<i>p</i> < 0.05
		10:10	2.70 ± 0.37				
		15:5	5.20 ± 0.42	9.74 ± 0.40	100.0	18	<i>p</i> < 0.001
	2POL-11 <i>n</i> = 10	5:15	2.80 ± 0.29	1.70 ± 0.23	16.0	18	<i>p</i> < 0.05
		10:10	4.20 ± 0.39				
		15:5	6.70 ± 0.54	11.84 ± 0.60	98.0	18	<i>p</i> < 0.001
	BIG30 <i>n</i> = 10	5:15	4.80 ± 0.13	1.92 ± 0.12	0.0	18	<i>p</i> < 0.001
		10:10	9.10 ± 0.35				
		15:5	13.30 ± 0.47	12.66 ± 0.16	42.0	18	<i>p</i> = 0.569
With pollen	Agrobio <i>n</i> = 10	5:15	1.70 ± 0.30	0.91 ± 0.17	25.0	18	<i>p</i> < 0.05
		10:10	2.30 ± 0.37				
		15:5	4.30 ± 0.54	8.96 ± 1.17	87.0	18	<i>p</i> < 0.01
	2POL-11 <i>n</i> = 10	5:15	2.70 ± 0.30	1.85 ± 0.29	26.5	18	<i>p</i> < 0.05
		10:10	4.00 ± 0.58				
		15:5	6.50 ± 0.54	12.07 ± 0.54	100.0	18	<i>p</i> < 0.001
	BIG30 <i>n</i> = 10	5:15	4.60 ± 0.16	1.90 ± 0.12	0.0	18	<i>p</i> < 0.001
		10:10	8.60 ± 0.37				
		15:5	12.90 ± 0.75	12.61 ± 0.20	40.0	18	<i>p</i> = 0.470

<sup>a</sup>Differences between observed and expected values within each row were compared using the Wilcoxon signed-rank test; two-tailed *p* values

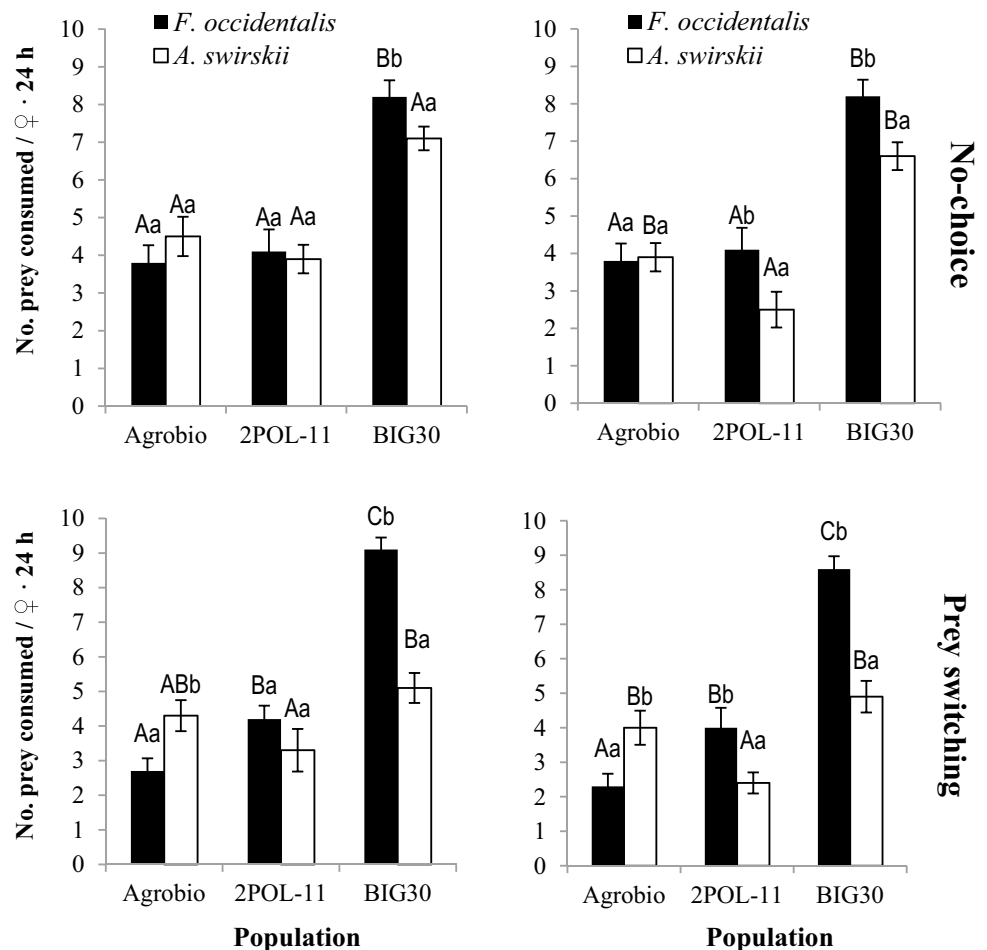
**Fig. 2** Total prey consumed (mean ± standard error) by a single *O. laevigatus* female from Agrobio, BIG30 and 2POL-11 populations in a choice situation between *F. occidentalis* and *A. swirskii* adults, with (right) or without (left) pollen supplementation (*n* = ten prey per female from each *Orius* population and for each pollen supplementation treatment). Different lowercase and uppercase letters above the bars indicate significant differences within and between populations, respectively (Wilcoxon signed-rank test, *p* < 0.05)



Comparing the results of these experiments with those obtained in trials in which females are presented with only one type of prey, either phytoseiid mites (previous section of this paper) or adult thrips (Mendoza et al.

2022), a fundamental difference is observed between our improved breeds and the commercial population (Fig. 3). Although total prey consumption is significantly higher in all cases when the two species are presented together

**Fig. 3** Number of adults (mean  $\pm$  standard error) of *F. occidentalis* (solid bars) and *A. swirskii* (blank bars) attacked by a single *O. laevigatus* female from Agrobio, BIG30 and 2POL-11 populations in no-choice situations (above, data for thrips adults from Mendoza 2022) versus a prey choice situation (below), with (right) or without (left) pollen as a supplement. Females ( $n=10$ ) were singled for 24 h with: ten adults of one prey species (no choice) or ten adults of each prey species (prey switching). Different lowercase and uppercase letters above the bars indicate significant differences within and between populations, respectively (Wilcoxon signed-rank test,  $p < 0.05$ )



rather than separately, both in the presence and absence of pollen, Agrobio females show a reduced consumption rate on thrips when it is supplied in a prey combination, while phytoseiid mortality remains at approximately the same level. In contrast, for both 2POL-11 and, especially, BIG30, females opt for IGP at a lower rate when they have the choice between the predatory mites and the adult thrips, while the predatory activity on the latter remains very high despite having the choice of IG prey.

No significant differences were observed in the mortality of the controls neither between both types of prey (signed-rank test:  $Z_{258} = 16,513.0$ ,  $p = 0.665$ ), nor between the different combinations of prey evaluated (multivariate ANOVA, *A. swirskii*:  $F_{1, 179} = 2.26$ ,  $p = 0.108$ ; *F. occidentalis*:  $F_{1, 179} = 1.69$ ,  $p = 0.18$ ), nor between both pollen treatments (multivariate ANOVA, *A. swirskii*:  $F_{1, 179} = 0.36$ ,  $p = 0.548$ ; *F. occidentalis*:  $F_{1, 179} = 0.01$ ,  $p = 0.904$ ). In any case, mortality of both phytoseiid mites and adult thrips mites was around 2.85% of the total prey, values practically negligible in comparison with those recorded in the presence of female *O. laevigatus*.

## Discussion

According to Murdoch's (1969) model, prey switching indicates a shift from less to more, according to an expected value, in the proportion of prey consumed by a predator with an increasing relative abundance of that prey. Such alternation is common in mobile predators that feed in several patches where there is a range in the proportion of available prey. This is the case of *O. laevigatus*, an insect with very good dispersal capacity in the crop, polyphagous and that feeds very frequently (Malais and Ravensberg 2003).

However, in the light of our experiments, at least as far as the commercial line Agrobio is concerned, *O. laevigatus* does not exhibit prey switching behavior between adult *A. swirskii* and adult *F. occidentalis*, but preferentially chooses the predatory mite when this prey is more or equally abundant than *F. occidentalis*. For females in this population, predation rates on thrips decrease when the predatory mite is added as an alternative prey, but



predation activity on *Amblyseius* do not decrease when they are present along with the adult thrips. This preference of *Agrobio* for the phytoseiid is possibly due to the difficulty to subdue a prey with greater avoidance ability such as the adult thrips, equipped with wings and higher mobility (Mouratidis et al. 2022). These results are in contrast to those observed by Madadi et al. (2008) between *O. albidipennis* and *N. cucumeris* in the presence or absence of *Thrips tabaci* (Lindeman), recording a significant preference of the anthocorid for the thrips. Particularly relevant were the results obtained by Chow et al. (2008, 2010) with commercial *O. insidiosus* populations on adults and second instar larvae of *F. occidentalis*. In their experience, *O. insidiosus* females followed a clear pattern of switching between both prey species (*F. occidentalis* and *A. degenerans* or *A. swirskii*) regardless of the stage of the thrips, preying proportionally more on the more abundant prey, which is in agreement with our results. Apart from the fact that they are different *Orius* species, it should be noted that our laboratory trials were conducted in a reduced and simplified setting such as 5 mL plastic vials together with a sample of plant material, while the previous ones were conducted as semi-field trials using whole sweet pepper plants, cucumber and eggplant in the case of Madadi et al. (2008) as well as stems and flowers of greenhouse-grown rose in the case of Chow et al. (2008). These differences might explain the slightly lower predation rates on thrips recorded in their case. Indeed, the fact that pollen is available in some plant structures (flowers) but not in others may lead to variation in the abundance of extraguild prey, IG prey and IG predator in flowers, fruits and leaves, which is expected to soften the intensity of trophic interactions (Janssen et al. 2007).

Regarding 2POL-11, the artificially selected population for an enhanced tolerance to pollen, it consumes the same amount of adult thrips when fed alone as in combination with the predatory mite, and on the contrary, the number of mites consumed per day is significantly lower when adult thrips are also present, especially when pollen is also added to the system as supplementary food. On the one hand, the high capacity of this population to obtain a nutritional benefit from non-prey resources (Mendoza et al. 2020a) makes it less dependent on feeding from one or another prey, and on the other hand, its hunting area is more limited to the area where pollen is added as a supplement (experimental observation), which it feeds on successfully but which is also used by mites and adult thrips. Be that as it may, in this case a preference for the predatory mite is not observed as it occurred with the commercial population *Agrobio*, and yet for this population the application of Murdoch's (1969) model does not support a real alternation between both types of prey, even though this is observed in practice (Fig. 1).

Surprisingly, it was just among the larger females, belonging to the enhanced line BIG30, that a real behavior adjusted to the prey switching model was registered, since the observed mortality rate of adult thrips is equal or even higher than expected at a high density with respect to that of the predatory mite. On the other hand, similarly to 2POL-11, the consumption of mites decreases in a situation of choice between both types of prey, while the consumption of thrips remains unchanged. In this case, the significantly larger size of BIG30 females allows them to choose between two prey, which they are able to subdue more easily than their smaller conspecifics, and their voracity is significantly higher. Hence, the choice of the adult thrips over the phytoseiid mite observed in practice may be motivated either by a lower encounter rate between the IG predator and the IG prey due to the niche specialization acquired by the former (and the impossibility for the phytoseiid mite to prey on the adult thrips), or by a simple question of nutritional requirement related to the difference in size between the predator and the two prey species. In this sense, many predators are opportunistic in their feeding strategy and do not show strong preferences for their prey species (Denno and Fagan 2003), while toxicity and size can influence prey selection (Polis et al. 1989). On the other hand, the prey switching behavior observed in BIG30 showed a similar pattern regardless of the addition of pollen or not as a supplement, since no significant differences were found between the two treatments in either prey preference or in the rate of IGP on *A. swirskii*. This absence of disruptive effect of pollen on IGP had already been observed by Shakya et al. (2009) in their experiments with strawberry plants, in which the predation rate of *O. laevigatus* on another phytoseiid mite, *N. cucumeris*, was not reduced in the presence of pollen, thereby contrary to their initial hypothesis.

According to the theory of intraguild predation, in the absence of food supplementation, two predators can coexist only if the IG prey is more efficient at exploiting the shared resource than the IG predator (Holt and Polis 1997). Whereas employing a non-prey resource such as pollen as a supplement allows the IG prey not to have to be superior in exploiting the original shared resource, as long as it has a higher ability to exploit the supplement than the IG predator (Daugherty et al. 2007; Wei 2019). Therefore, in the case of pollen as supplementary food, stable coexistence of the two predators is possible when the IG predator is more proficient at exploiting the shared herbivorous prey as long as the IG prey is mostly phytophagous. Well, the addition of pollen provides a solution to the coexistence problem in the case of the omnivorous predators *O. laevigatus* and *A. swirskii*, with phytoseiid mites being efficient pollen eaters (Goleva and Zebitz 2013; Calvo et al. 2015; Janssen and Sabelis 2015) and *O. laevigatus* being an efficient thrips predator. Nevertheless, our results suggest that the ability

of the IG predator to exploit pollen as food is also particularly relevant in mediating compatibility with *A. swirskii*. In fact, although the addition of pollen may increase the encounter rate between *A. swirskii* and *O. laevigatus* as a resource that can be used by both, only among females of the enhanced pollen-tolerant strain, 2POL-11, there was a significant reduction in the strength of IGP with pollen. In any case, this intraguild coexistence mediated by pollinivory may be an advantage for the use of *O. laevigatus* as an augmentative biological control agent in pollen-producing crops but also in less or non-pollen-producing crops when supplemental feeding strategies are involved. For example, in chrysanthemum crops *Typha* pollen is frequently sprinkled on flowers as an additional food source, thus favoring coexistence among predatory mites and thus reinforcing control of *F. occidentalis* populations (Skirvin et al. 2006; Hoogerbrugge et al. 2008). On the other hand, in cucumber crops where plants are parthenocarpic and therefore with low pollen availability, the use of a supplementary food, consisting either of some alternative prey or pollen, has been proposed in order to improve the efficacy of natural enemies after release (Messelink et al. 2014; Oveja et al. 2016). These examples could provide a good precedent for the application of our improved pollen-tolerant *Orius* strain in this type of crops as well as its coexistence with *A. swirskii*. Since *Orius*, when released in an established crop, is distributed in foci, food could also be provided locally in these same foci where predators are released. This will allow predators to hoard food and reduce the risk of resources being used for pest population increase, as suggested by van Rijn (2002). Furthermore, Leman and Messelink (2015) showed that, although *F. occidentalis* feeds on pollen, the increased predator population as a consequence of the presence of this food improves the predator–prey relationship and is a long-term benefit for biological control.

In any case, the benefits of pollen addition (or its natural presence) in biological control have long been reported in the literature. For example, Sabellis and van Rijn (1997) demonstrated that a weekly supply of almost 3 g of *Typha* pollen to cucumber plants allowed *A. degenerans* to reach adulthood, promoting the abundance of juvenile and adult phytoseiids and thus significantly contributing to thrips control. Similarly, Matsumura et al. (2004) extensively discussed the improvement in the performance of a predator by IGP as a consequence of higher nitrogen intake from the IG prey with higher nitrogen content than the herbivorous prey. On a more practical basis, a very important contribution to the implementation of pollen addition programs came from the study by Shakya et al. (2010), who demonstrated how pollen availability and the simultaneous activity of two predators (*O. laevigatus* and *N. cucumeris*) can modify decision-making in pest management, drastically reducing the use of costly and damaging insecticides. Lastly, assuming pollen as

“prey” or alternative food for both the phytoseiid mite and the anthocorid, with its addition to the crop, it would become a stabilizing element of the population dynamics of both predators, as already modeled by Wei (2019) to analyze the possible effects of prey alternation on the intensity of IGP.

Regarding our improved genetic line for a larger body size and therefore for a greater predatory capacity, the reduction in the intensity of predation on IG prey compared to the observed increase in pressure on adult thrips has a substantial effect on the control of the populations of this species in the short term, but also in the long term in regard to biological control in general, since a more relieved coexistence with *A. swirskii* allows the development of its populations, avoiding the potential resurgence and development of another key pest such as the greenhouse whitefly. In other words, the niche differentiation acquired by this predator when feeding on thrips adults might allow shifting from a strong IGP interaction to a resources exploitation competence among predators or simply to more independent trophic chains. In both cases, together with the possibility of coexistence with *A. swirskii*, the result could be a greater strength of interaction with the initial prey. Therefore, the high predatory capacity acquired by these insects as a consequence of the selection process could be a substantial advantage when using them as a tool for inundative biological control, very effective in circumstances of an uncontrolled increase in thrips populations. This occurs because *Orius* predation on *A. swirskii* can occur without the necessity of thrips death (Rosenheim et al. 1995), as the two predators can encounter each other while feeding randomly in a shared environment. Therefore, the success of this combined system will depend on the relative abundance of the phytoseiid mite and the adult thrips (Polis et al. 1989; Holt and Huxel 2007), so that in circumstances where inundative release would become necessary, our enhanced population for a larger body size would be able to control pest population peaks without endangering biological control due to a significant effect on the IGP on *A. swirskii* that would not be present in this case.

The results of our experiments are particularly relevant in terms of the degree of IGP observed if we take into account that most of the observations made on this phenomenon came from laboratory experiments using very small settings (Cloutier and Johnson 1993) or small spaces in the field (Rosenheim et al. 1993). Under these conditions, predators can only feed on each other while sharing the same prey. However, under greenhouse conditions, IGP may be less intense due to several reasons. First, a higher density of the target prey may reduce the rate of predation between the two predators (Gillespie and Quiring 1992; Cloutier and Johnson 1993). Second, the plant itself can provide refuges, such as domatia, which are frequently occupied by *A. swirskii* and help them avoiding other top predators such as *O. laevigatus* (Schmidt 2014). Third, the target prey may create

shelters that help a sufficiently small predator escape from larger predators. An example of that could be thrips-induced galls (Sabelis and van Rijn 1997), which can be invaded by predatory thrips and phytoseiid mites, but not by a predator such as *Orius*, especially if the latter has been genetically enhanced for larger size, as is the case with BIG30. Moreover, both predators can avoid each other by fragmenting the spatial niche and habitat structure or by the presence of an alternative resource. By feeding on different prey or thanks to pollen supplementation, phytoseiids would have temporary refugia (Weintraub et al. 2007) and both they and the top predators, in this case *O. laevigatus*, could be distributed separately within the plant, reducing the encounter rate between them and facilitating coexistence (Janssen et al. 2007; Bouagga et al. 2018). In any case, if avoiding intraguild predation remains the rule rather than the exception, the reduction in the intensity of the predation rate of *O. laevigatus* on *A. swirskii* observed in the laboratory for our breeding lines should only become more evident under field conditions, so that coexistence between the two predators could be expected to have an additive effect on the suppression of thrips populations and other key pests such as whiteflies, favoring the success of biological control. However, more experiments will be necessary to confirm this hypothesis.

## Conclusions

In conclusion, the results of our trials with *A. swirskii* have allowed us to demonstrate, on the one hand, that our enhanced *O. laevigatus* populations for larger size and higher pollen tolerance have a greater preference for adult thrips than the females of a commercial population, resorting to intraguild predation less frequently. On the other hand, the addition of pollen to the tritrophic system comprised by both predators and adult thrips has a positive effect on the coexistence between the predators, especially in the case of the pollen-tolerant population. Therefore, these two improved lines are tools that could have a very significant impact on the integrated control of thrips in situations where coexistence with *A. swirskii* is seriously compromised, such as at the beginning of the crop or in conditions of absence or low prey level.

## Author contributions

PB conceived research. JEM and PB designed experiments. JEM, VB, ARG and DC collected and prepared material. JEM, VB and ARG conducted experiments and collected data. PB supervised experiments. JEM analyzed data. JEM and PB wrote the manuscript. All authors read and approved the manuscript.

**Acknowledgements** This research was funded by Grant PID2020-116897RB-I00 funded by Ministerio de Ciencia e Innovación and Agencia Estatal de Investigación MCIN/AEI/<https://doi.org/10.13039/501100011033>. The A.R.-G. contract was co-financed by the R&D Support Plan of the Polytechnic University of Cartagena. J.E.M. held a grant from the MSIU (FPU14/02932). The V.B. contract was financed by grant PDC2021-121383-I00 funded by Ministerio de Ciencia e Innovación and Agencia Estatal de Investigación MCIN/AEI/<https://doi.org/10.13039/501100011033> and European Union Next Generation EU/PRTR

**Funding** Open Access funding provided thanks to the CRUE-CSIC agreement with Springer Nature. Grant PID2020-116897RB-I00 funded by Ministerio de Ciencia e Innovación and Agencia Estatal de Investigación MCIN/AEI/<https://doi.org/10.13039/501100011033>. José Enrique Mendoza holds a grant from the MSIU (FPU14/02932). Amador Rodríguez-Gómez contract was co-financed by the R&D Support Plan of the Polytechnic University of Cartagena. The Virginia Balanza contract was financed by grant PDC2021-121383-I00 funded by Ministerio de Ciencia e Innovación and Agencia Estatal de Investigación MCIN/AEI/<https://doi.org/10.13039/501100011033> and European Union Next Generation EU/PRTR.

## Declarations

**Conflict of interest** The authors declare an agreement with the bio-producer Agrobio to commercialize the artificially selected strains of *Orius laevigatus*.

**Availability of data and material** The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.

**Code availability** Not applicable.

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