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RESEARCH

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Predation preference and nutritional values of four different aphid species for *Orius sauteri* (Hemiptera: Anthocoridae)

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Abstract

Background: *Orius sauteri* (Poppius) is one of the important natural enemies of aphids in Asia. Understanding its predation preference and efficiency can help improve its effectiveness as a biological control agent. Here, the predation preference of *O. sauteri* adults toward *Aphis craccivora* Koch, *Rhopalosiphum maidis* (Fitch), *Myzus persicae* Sulzer, and *Aphis gossypii* Glover was studied.

Results: The research found that *O. sauteri* had good predation efficiency on four important aphid species. *Orius sauteri* killed a similar number of four aphids in non-selective tests, but it preferred to eat more *R. maidis* and *A. gossypii*, and fewer *A. craccivora* in selective tests. The main biochemical components of the four aphid species were analyzed, including water content and nutritional components along with body mass. *Rhopalosiphum maidis* had a significantly lower water content than *A. craccivora*. *Orius sauteri* preferred *R. maidis* and *A. gossypii*, which harbored higher lipid and trehalose content, while preying on fewer *A. craccivora*, which had a larger body weight for the supplement of water and nutrition. The predation preference may be due to the closest nutrition composition to the optimal intake of *O. sauteri*.

Conclusions: This study showed that the predatory selection of *O. sauteri* was closely associated with the water content, bodyweight, lipid, and trehalose levels of prey, while the glycogen content and protein level might be less determinant. The high predation capacity on four aphids of *O. sauteri* indicated the great potential to integrate this predator into biological control strategies against aphids.

Keywords: Aphids, *Orius sauteri*, Prey preference, Nutritional analysis, Trehalose

Background

Studying predators' behavior is important to understand how the predators live and how they affect the population dynamics of their prey (Dixon 2000). Predators attack prey selectively and feed on a subset of prey that they encounter (Waldbauer and Friedman 1991; Klecka and Boukal 2012). According to the optimal foraging theory, individuals behave in a way to obtain food resources required for survival and reproduction while expending the least amount of time (Pyke et al. 1977), which posits that predators should maximize their energy intake by selectively preying on the most beneficial resources. The energy obtained from prey has been the main prey currency influencing the foraging behavior of predators (Whelan and Schmidt 2007). However, this theory fails when applied to predator species that feed on moving prey or place excessive emphasis on their energy intake instead of the prey's nutritional composition (Sih and Christensen 2001; Kohl et al. 2015). Predators do not use prey only as a source of energy, but also to obtain building blocks for their tissues (Raubenheimer et al. 2009). More recently,

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studies have documented that water and nutrients, including carbohydrates, proteins, and lipids, play important roles in animal foraging decisions and food-web ecology (Fagan et al. 2002; Sterner and Elser 2002; McCluney and Sabo 2009, 2016; Schmidt et al. 2012; Simpson and Raubenheimer 2012; Wilder et al. 2013; Allen et al. 2014; Deguines et al. 2017; McCluney 2017).

The minute pirate bug, *Orius sauteri* (Poppius) (Hemiptera: Anthocoridae), is an important biological control agent for numerous agricultural pests in Asia (Yano 1996; Yano et al. 2005). *Orius sauteri* can regulate many economically important arthropod pests, including mites (Sun et al. 2009), whiteflies (Yano et al. 2005; Wang et al. 2013), thrips (Nagai and Yano 2000; Liu et al. 2011a), and aphids (Nakata 1995). Notably, *O. sauteri* often appears in corn and cotton fields feeding on aphids and thrips (Cui 1994; Zou 2004).

Aphids (Hemiptera: Aphididae) are important agricultural pests and pose a serious threat to the quality and yield of crops, causing huge economic losses. In addition to causing direct damage through their feeding behavior, aphids also transmit plant pathogenic viruses. The cosmopolitan cowpea aphid, *Aphis craccivora* (Koch), is a holocyclic, heteroecious species that infests eight plant families and transmits over fifty kinds of plant viruses (Stoetzel and Miller 2001). Yield loss of more than 50% occurs when high infestations of cowpea aphids are not controlled in the production of cowpea (Obopile 2006). The corn leaf aphid, *Rhopalosiphum maidis* (Fitch), is the most economically damaging aphid pest on maize and an important vector of several destructive maize viruses, including barley yellow dwarf virus, maize yellow dwarf virus, sugarcane mosaic virus, and cucumber mosaic virus (El-Muadhidi et al. 2001; Hawkes and Jones 2005; Jarosova et al. 2013; Power et al. 2011; Krueger et al. 2013). The cotton aphid, *Aphis gossypii* Glover, is a polyphagous herbivore that causes serious damage to many plants, including cucumber (*Cucumis sativus* Linn), okra (*Abelmoschus* spp.), and cotton (*Gossypium herbaceum* Linn) (Zhang et al. 2020). The green peach aphid or peach potato aphid, *Myzus persicae* Sulzer, is a worldwide distributed aphid crop pest. It is highly polyphagous, with a host range of more than 400 species in 40 different plant families, and causes indirect damage to its host by its capability of transmitting over 100 different plant viruses (Blackman and Eastop 2000).

The aim of the present study was to study the preferences of the predatory *O. sauteri* on four different aphids, *A. craccivora*, *R. maidis*, *M. persicae*, and *A. gossypii*, which are all important aphids. Also, explore the reasons behind the selective predation of the aspects of water content, body weight, and nutritional components.

Methods

Insects rearing

Original colonies of *O. sauteri* were collected from corn plants in the China Agricultural University's experimental field in Beijing, China. Laboratory colonies of *O. sauteri* were fed on *Sitotroga cerealella* (Olivier) eggs attached to Post-it notes along with green bean pods for oviposition, with some buckwheat hulls as shelter. Insects were reared in an incubator under conditions of 25 ± 2 °C, 70 ± 5% R.H. (relative humidity), and 16:8 h (L:D) photoperiod cycle (Ge et al. 2018). Colonies of four aphid species were originally initiated with insects collected from the experimental field of China Agricultural University. *Aphis craccivora* was mass reared on broad bean plants (*Vicia faba* L.). *Rhopalosiphum maidis* was reared on the corn plants. *Aphis gossypii* was reared on cotton plants, and *M. persicae* was reared on pepper seedlings. The host plants were grown in plastic pots filled with a mix of nutrient soil and vermiculite (1:1). All of the aphid colonies were kept in a controlled chamber (20 ± 1 °C, 75 ± 5% R.H., 16L:8D). Nymphal aphids were used for the experiments.

Non-selective and selective predation of *Orius sauteri*

In all predation experiments, as suggested by Nakamura (1977), the 3-day-old female of *O. sauteri* adults was individually placed in vials and starved for 24 h before the experiment to maximize individual hunger levels. The nymph aphids were introduced in plastic Petri dishes (diameter = 9 cm) before the predator so that they could disperse and the predators might have to search for the aphids. The predator was removed from the dish, and the number of aphids killed by the predator was recorded in each Petri dish after 24 h. All these experiments were performed at 25 °C, 65 ± 5% R. H. and a photoperiod of 16L:8D.

For the non-selective predation assay, 60 individuals of each of the four different aphid species were assayed separately. The predators were introduced individually into the Petri dishes which contained specific amounts of aphids per Petri dish along with corresponding host plant leaves.

For the selective predation assay, fifteen aphids of similar body size to each species were mixed together as prey. *Orius sauteri* was introduced individually into the Petri dishes for predation.

Aphids' weight and water content

A group of 50 aphids of each species of similar body size was collected in different sample vials. The fresh weight of each sample was measured using an electronic scale (TP-114, Denver Instrument, USA). The dry weight of four aphid species was obtained by oven drying at 65 °C until a constant weight was achieved, and then, water content was calculated. These aphids were used for total lipid, glycogen, trehalose, and soluble protein content analyses as well. There were nine replicates for each aphid species.

Nutritional components analysis

The total lipid, glycogen, trehalose, and soluble protein of the four aphid species were extracted based on a slightly modified extraction method of Zhou et al. (2004) and Shi et al. (2010). Total lipid was assayed by using a triolein (Sigma-Aldrich, St. Louis, MO, USA) as a quantitative standard (Van Handel 1985b; Van Handel and Day 1988). The glycogen and trehalose content was measured using the anthrone method (Van Handel 1985a) with glycogen and trehalose standards purchased from Sigma Chemical Co. Soluble protein was determined by the method of Shi et al. (2010) using the BCA Protein Assay Kit (Biosynthesis Biotechnology Company, Beijing, China). The total lipid, soluble protein, glycogen, and trehalose content of different aphid species was quantified separately by a spectrophotometer at a 525 nm, 562 nm, 625 nm, and 625 nm wavelength, respectively. There were five to nine replicates of different aphid species for each nutrient.

Statistical analysis

The predation capability of *O. sauteri*, water content, fresh and dry weights, and nutritional contents against the fresh weight of four aphid species was compared by one-way analysis of variance (ANOVA) followed by LSD (Least Significant Difference) test with $\alpha = 0.05$. All data were analyzed using SPSS V20.0. (IBM Corp., Armonk, NY, USA).

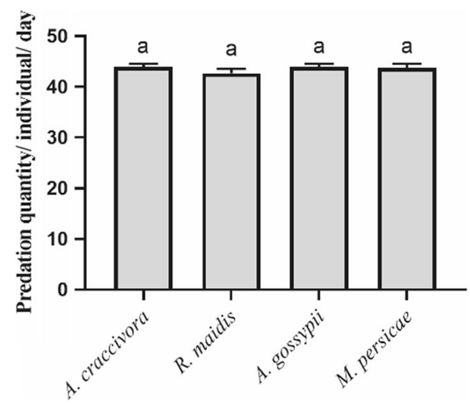

Fig. 1 Non-selective predation of *Orius sauteri* on the four aphid species. Values are mean ± SE (Standard Error). The data were compared by ANOVA followed by LSD test with $\alpha = 0.05$, and means indicated by the same letter are not significantly different

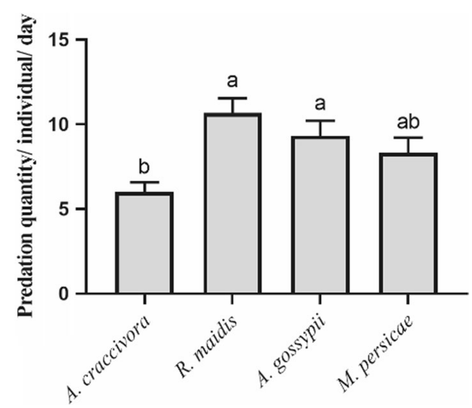

Fig. 2 Selective predation of *Orius sauteri* on the four aphid species. Values are mean ± SE. The data were compared by ANOVA followed by LSD test with $\alpha = 0.05$, and means indicated by the same letter are not significantly different

Results

Non-selective and selective predation of *Orius sauteri*

The results indicated that there was no significant difference among the predation capabilities of *O. sauteri* on *A. craccivora*, *R. maidis*, *M. persicae*, and *A. gossypii* in the non-selective experiment ($F_{3,11} = 0.717$, $P = 0.569$; Fig. 1). However, *O. sauteri* females showed a significant predatory preference in the selective test ($F_{3,11} = 5.819$, $P = 0.021$; Fig. 2). *Orius sauteri* killed the largest number of *R. maidis* and the fewest *A. craccivora* among the four species. There was a remarkable difference in the consumption of *O. sauteri* by *A. craccivora* compared to *R. maidis* and *A. gossypii*.

Water content and bodyweight of four aphid species

The water content of *R. maidis* (67.40%) was significantly lower compared to *A. craccivora* (75.77%), *M. persicae* (79.91%), and *A. gossypii* (75.30%) ($F_{3,35} = 9.107$, $P < 0.001$; Fig. 3a). There was no significant difference among these three aphid species.

The rank of fresh and dry weights of four aphid species showed similar patterns. The fresh and dry weight of *A. craccivora* was both the highest among the four aphid species, and they were significantly higher than the other three aphid species. (Fresh weight: $F_{3,35} = 207.432$, $P < 0.001$; Fig. 3 b; Dry weight: $F_{3,35} = 260.861$, $P < 0.001$; Fig. 3c). The fresh and dry weight of *R. maidis* was significantly higher than those of *M. persicae* and *A. gossypii,* and there were

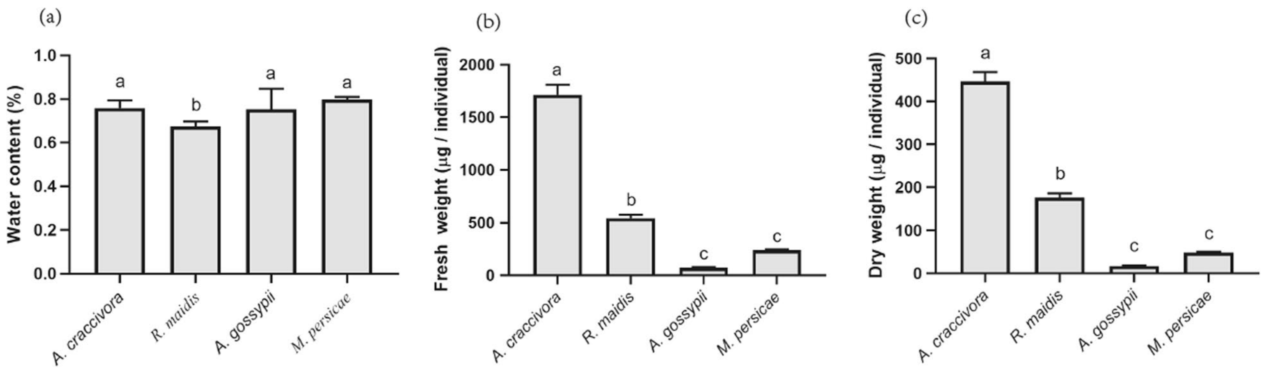

Fig. 3 Water content (**a**), fresh (**b**) and dry (**c**) body weights of four aphid species. Values are mean ± SE. The data were compared by ANOVA followed by LSD test with $\alpha = 0.05$, and means indicated by the same letter are not significantly different

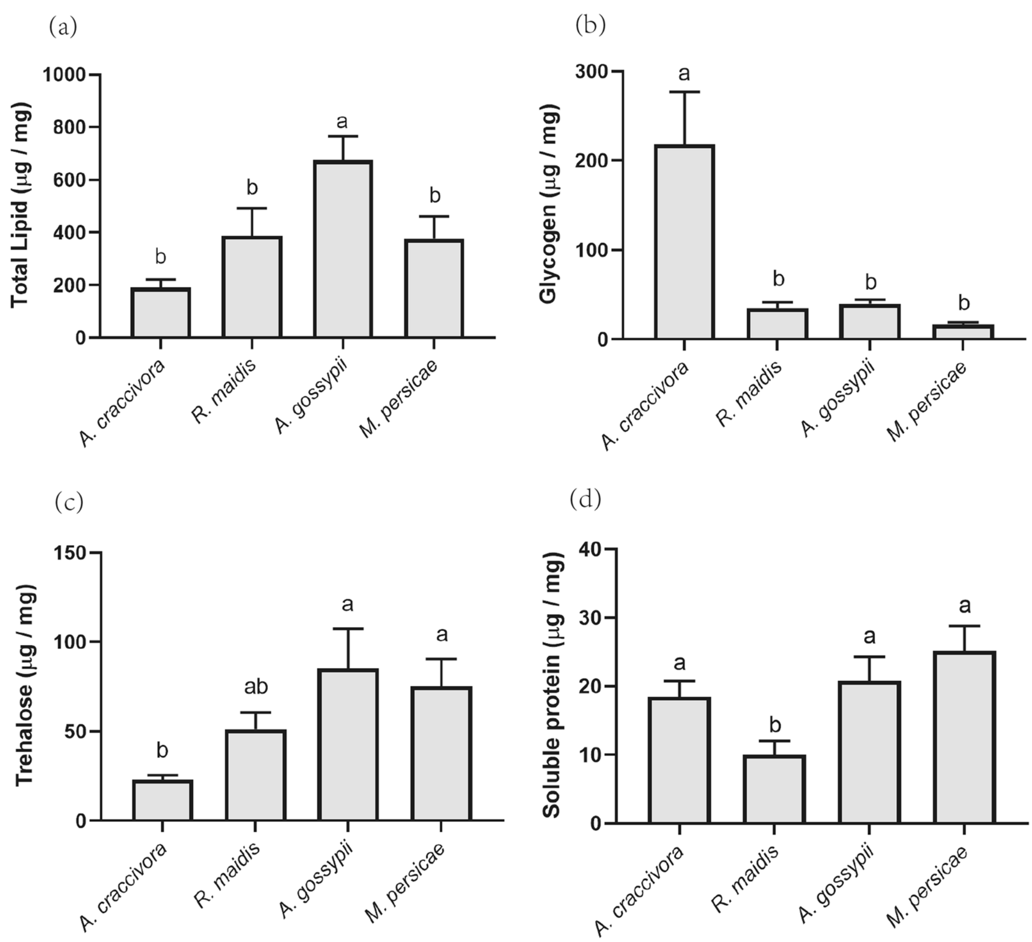

Fig. 4 Total lipid (**a**), glycogen (**b**), trehalose (**c**), and soluble protein (**d**) content (ug/mg fresh weight) of four aphid species (total lipid: $n = 6$–9; glycogen: $n = 8$–9; trehalose: $n = 5$–9; soluble protein: $n = 6$–9). Values are mean ± SE. The data were compared by ANOVA followed by LSD test with $\alpha = 0.05$, and means indicated by the same letter are not significantly different

no significant differences between *M. persicae* and *A. gossypii.*

Nutritional components of four aphid species

The total lipid level against an aphid's fresh weight in *R. maidis* and *A gossypii* was significantly higher than that in *A. craccivora* ($F_{3,31} = 3.629$, $P = 0.025$; Fig. 4a). The total lipid level in *Aphis craccivora* was the lowest, but it was not different from that in *M. persicae*. *Aphis craccivora* showed a significantly lower trehalose level than the other three aphid species ($F_{3,30} = 3.855$; $P = 0.020$; Fig. 4c). In addition, *A. craccivora* contained 5–16 higher glycogen levels than the other three aphid species ($F_{3,34} = 11.318$; $P < 0.001$; Fig. 4b). There was no significant difference in soluble protein content among the four aphid species ($F_{3,29} = 1.264$; $P = 0.307$; Fig. 4d).

Discussion

Orius sauteri, as a generalist predator, demonstrated remarkable behavioral and physiological adaptability in response to a variety of food resources (Liu et al. 2011a, b). Previous research has shown that aphids are an appropriate prey for *O. sauteri* (Wang et al. 2014). In this study, *O. sauteri* females had similar predation capabilities on *A. craccivora, R. maidis, M. persicae, and A. gossypii* in the non-selective experiment. Alvarado et al. (1997) reported the maximum consumption of *Orius laevigatus* (Fieber) and *Orius majusculus* (Reuter) on *A. gossipii* was 17 ± 2.09 and 21.1 ± 2.41, respectively, in 24 h., which is apparently lower than our results (44.0 ± 0.58; Fig. 1). Ge et al. (2018) tested the predation of *A. craccivora* by *O. sauteri* under different temperatures, and the consumption was similar to present study results in the same condition and prey density. Based on these results, we assume that *O. sauteri* does present strong predation on these aphids even compared with other important predators of Anthocoridae species. Surprisingly, there was no significant difference in the consumption of *O. sauteri* in 24 h on four aphid species, which could be explained by *O. sauteri*'s behavioral and gustatory suitability to these four aphid species. When *O. sauteri* was provided with prey options, notably higher consumption of *R. maidis*, and *A. gossypii* was identified compared to *A. craccivora*. However, it has not been reported on the biochemical mechanism of the selective predation of *O. sauteri* adults on these four aphid species. Here, we studied the main biochemical components of the four aphid species, including water content and nutritional components along with bodyweight. The result showed that the predatory selection of *O. sauteri* was closely related to the water content, body weight, lipid, and trehalose content of prey, while glycogen and protein content might be less determinant in this case.

Orius sauteri is a small piercing-sucking predator. Thus, the water content and body size of prey are important for prey selection. *Rhopalosiphum maidis,* with a significantly lower water content compared to the other three aphids, may contain more necessary nutrient substances to meet the demands of specific nutritional requirements for the development of predators. Compared to *A. craccivora,* which has the largest body size, and the heaviest body mass, the other three relatively small-sized aphids seemed to be easier captured by *O. sauteri*. The finding of Farhoudi et al. (2014) showed that aphid size is a more important factor than color in contributing to the predation preference of *Aphidoletes aphidimyza* (Rondani). Predators and parasites usually select small prey as preferred food, and that might be due to the low defensive capabilities and short handling times (Allan et al. 1987; Reitz et al. 2006). In addition to the size of prey, predation characteristics like prey handling ability and prey encounter rate are considered to be positively influenced by the size of the predator (Farhoudi et al. 2014). *Orius sauteri*, as the predator in our research, which has a small body size might try to avoid relatively large prey which is consistent with many previous studies (Schmidt et al. 2012; Farhoudi et al. 2014; Allan et al. 1987Reitz et al. 2006).

The extremely high glycogen content in *A. craccivora* might not contribute to the predation preference of *O. sauteri*, which suggests the glycogen content in other aphid species can meet the demands of *O. sauteri*. The nutrient composition (carbohydrates, proteins, lipids) of prey, its elemental composition such as the C:N:P ratio, or essential micronutrient content such as the long-chain polyunsaturated fatty acids relative to the needs of a predator thus provides a more realistic basis for studies of selective predation (Guo et al. 2018). Previous researchers hypothesized that multiple nutrient compositions close to the predator's optimal demands which include some particularly rich critical nutrients may contribute to the preferred predation (Schmidt et al. 2012; Raubenheimer and Simpson 2003). Thus, *R. maidis* and *A gossypii,* as the preferred preys of *O. sauteri* among the four aphids, might have a nutrient composition that is closest to the optimal intake composition of *O. sauteri*. The total lipid level against an aphid's fresh weight in *R. maidis* and *A gossypii* was significantly higher than that in *A. craccivora*, and that is consistent with the predational preference of *O. sauteri* adults. *Orius sauteri* showed less preference to *A. craccivora* probably because of their low content of some particular crucial substances such as lipid and trehalose. Different prey species exert distinct effects on the development and reproduction of predators, which may contribute to the preference of predators on prey (Calixto et al 2013). The physiological and nutritional mechanisms need to be explored further (Raubenheimer et al. 2009; Mayntz and Toft 2001). There is accumulating evidence that nutrition has a prominent influence on trophic interactions, and combining more detailed dietary information with studies of food webs could give us a much deeper understanding of the structure and function of communities and ecosystems (Muller-Navarra 2008). The feeding preference of *O. sauteri* is likely to be correlated with the profitability of energy substances in its metabolic processes. It has been proved that trehalose is the dominant sugar in the hemolymph and other tissues of insects as it provides energy for targeted activities (Van Handel 1969; Lu et al. 2019). Egg-laying by insects is closely related to trehalose levels. Huang and Lee (2011) found that the production of oocysts would be delayed by decreasing trehalose levels, suggesting that trehalose is a key energy source during spawning. The addition of an appropriate amount of trehalose or glucose may have a positive effect on the growth, development, and reproduction of *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) (Li et al. 2020). Schmidt et al. (2012) found the spider *Pardosa milvina* (Araneae: Lycosidae) could discriminate against different prey based only on their nutrient content. The activity of insects has a close relationship with their energy metabolism (Wong et al. 2016). Predators are sensitive to their nutritional needs, and based on that, predators decide whether to capture a particular prey or not so as to regulate the amount of their food intake to satisfy their metabolic needs (Mayntz et al. 2005). Li and Jackson (1997) demonstrated that there are long-term benefits for predators in many aspects when predator *Portia fimbriata* (Araneae: Salticidae) feeds on preferred prey, such as a faster developmental rate, larger body size at maturation, and especially a higher survival rate than when feeding on less-preferred prey. Considering these, the preferred prey chosen by *O. sauteri* might also have long-term potential physiological benefits for the predator.

The protein leverage effect hypothesis predicts that consumers will not stop feeding until they reach the intake level of a specific target protein (Raubenheimer et al 2009; Simpson and Raubenheimer 2005). Thus, consumers have to hunt more prey in order to maintain protein intake and get similar amounts of protein obtained from higher protein level prey. The finding of Farhoudi et al. (2014) showed that predatory gall midges consumed more red aphids, which have lower protein levels (Ahsaei et al. 2013) than green ones of the same size. Here, we found that *R. maidis* had the lowest protein level among the four aphids. However, the content may have a negligible effect on the prey preference of *O. sauter*i in this study, because there was no significant difference in soluble protein content among the four aphid species. Generally, females of *Orius* spp. consume significantly more prey and have a bigger effect on the offspring than males do (Tanaka et al. 2002). However, further studies on sex differences in selective predation may be needed to get a better understanding of the foraging behavior of *O. sauteri*.

We also found that the number of prey corpses was merely partially consumed, which suggests that *O. sauteri* killed extra aphids than they could consume. Similar findings were also reported in other studies (Alvarado et al. 1997; Lang and Gsodl 2003; Maupin and Riechert 2001). For example, Alvarado et al. (1997) found prey *A. gossipii*, which was predated by four predatory bugs, was killed and partially consumed. Superfluous killing behavior was also found in spiders, and it was presumed that the superfluous killing behavior indicates the predators' adaptation to food-limited environments (Maupin and Riechert 2001). This predatory behavior of *O. sauteri* in one way or another may contribute to better control of aphids in the field. Further studies are needed to check the numbers and status of corpses for different preys, and the handling abilities of different preys, which will help us get a better understanding of the feeding habits of *O. sauteri*.

Conclusions

In conclusion, *Orius sauteri* had good predatory effects on four important aphid species. Predatory selection was closely associated with the differences in body size, water and nutritional content, especially the lipid and trehalose levels of different aphid species. Females of *O. sauteri* preferred *R. maidis* and *A. gossypii*, which contain significantly more lipid and trehalose than *A. craccivora*. *R. maidis* also has lower water content. Our research may help understand the biochemical mechanism of selective predation of *O. saureri,* and tries to prompt further evaluation of the predatory potential of *O. sauteri* as an effective biological control agent for four important aphids. Further studies of predatory interaction between *O. sauteri* and its prey need to be thoroughly explored in the future.

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Authors' contributions
TL involved in conceptualization; TL took part in methodology; TI involved in validation; LZ and ZQ took part in formal analysis; ZQ, KC, and TL took part in investigation; YG and YW involved in resources; LZ took part in writing—original draft preparation; WS and LZ involved in writing—review and editing; LZ involved in visualization; WS took part in supervision; WS took part in project administration; WS involved in funding acquisition. All authors have read and agreed to the published version of the manuscript.

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Availability of data and materials
The datasets used and/or analysed during the current study are available fromthe corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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