

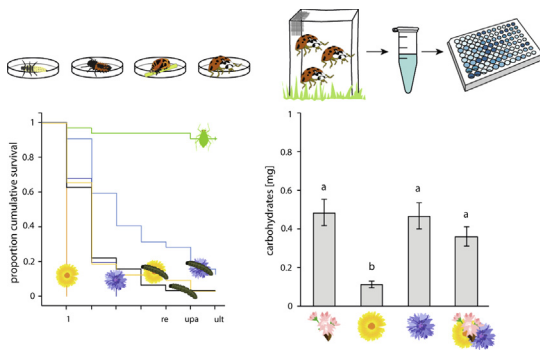


Utilization of plant-derived food sources from annual flower strips by the invasive harlequin ladybird *Harmonia axyridis*

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GRAPHICAL ABSTRACT



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ABSTRACT

The ability to utilize plant-derived food sources and suboptimal prey when the main prey is scarce may enhance competitiveness and invasiveness of entomophagous species such as *Harmonia axyridis*. Alternative food sources are particularly abundant in flower strips and other agri-environment schemes to promote biodiversity and may thus also benefit the invasive species. We investigated the effects of alternative food sources on the development and reproduction of *H. axyridis*. Laboratory experiments demonstrated that larvae of *H. axyridis* developed into adults and produced offspring when reared solely on aphids, lepidopteran eggs or maize pollen but not when they were fed only lepidopteran caterpillars or buckwheat flowers. When fed a combination of the latter two suboptimal food sources, however, some *H. axyridis* larvae developed into fertile adults. Flowering plant species differed in their food quality to sustain ladybird survival and development when fed alone or in combination with suboptimal prey. Differences in food quality of flower species were confirmed in field-cage studies where newly emerged adults were exposed for six days to different plant species and their energetic compartments were analyzed subsequently. Overall *Fagopyrum esculentum* and *Centaurea cyanus* provided a higher food quality than *Calendula arvensis* in those experiments and mixing flower species did not provide an additional benefit. The results show that the harlequin ladybird can sustain itself not only on optimal prey, but also utilize alternative, animal- and plant-derived diets. This could provide *H. axyridis* a competitive advantage over those native ladybird species that depend on aphids for their reproduction.

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1. Introduction

The predacious harlequin ladybird *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) is native to central and eastern Asia (Dobzhansky, 1933). It has been imported and released for aphid biological control in the United States as early as in 1916 (Gordon, 1985) and in Western Europe first in 1990 (Coutanceau, 2006). After a time lag of several years the species established and spread rapidly with its current distribution including North and South America, Africa, and Europe (Brown et al., 2008; Roy et al., 2016). *H. axyridis* is a strong competitor and populations of several native coccinellid species have markedly declined since its arrival (Brown et al., 2011; Roy et al., 2016) although in certain regions declines began before the arrival of *H. axyridis* (Honek et al., 2016).

One factor for the success of the harlequin ladybird seems to be its particularly wide dietary range, compared to many other ladybird species (Roy et al., 2006). While many primarily aphidophagous ladybird species also accept alternative prey such as lepidopteran and coleopteran larvae, the suitability of the alternative food sources varies greatly among prey and ladybird species (Evans, 2009). Furthermore, plant derived food sources such as pollen, floral and extra floral nectar, fruits and even foliage can be utilized to different extents as additional or alternative food sources (Berkvens et al., 2010; Lundgren 2009a,b). These plant-derived food sources can be used to build up energy reserves before hibernation (Ricci et al., 2005) or to survive when prey is scarce (Lundgren, 2009a). Those situations occur frequently as e.g. aphid populations fluctuate strongly due to weather conditions or due to the fact that they have been exploited by other natural enemies (Hodek & Michaud, 2008). However, only a few species of aphidophagous ladybirds such as *Coleomegilla maculata* De Geer and *H. axyridis* are able to complete development solely on plant food sources (Berkvens et al., 2008; Lundgren & Wiedenmann, 2004). For those ladybirds, and in particular their less mobile larvae, the ability to utilize plant-derived food sources results in a strong competitive advantage.

While a large proportion of the Central European land cover is characterized by managed agricultural ecosystems, many European countries have implemented agri-environmental schemes that foster the establishment of semi-natural habitats for the provision of additional resources to enhance biodiversity. Within these habitats different forms of sown flower strips are increasingly being established (Jacot et al., 2007; Marshall & Moonen, 2002). A number of studies found that insect abundance in such flower strips is higher than in the crop habitat (reviewed in Haaland et al., 2011) and studies from the UK (Ramsden et al., 2015) and from Switzerland (Tschumi et al., 2014) reported high numbers of coccinellids in flower strips. While this is desired for native species, flower strips may at the same time also provide resources for the invasive *H. axyridis*. In fact, *H. axyridis* has been observed as the second most abundant species (after *Propylea quatuordecimpunctata* L.) in several flower strips in Switzerland (Tschumi and Albrecht, personal communication) and in Belgium (Hatt et al., 2017).

Thus, the present study aims to investigate whether and to what extent *H. axyridis* can profit from these additional food sources by unraveling the fitness consequences that result from the utilization of several floral resources commonly found in flower strips. In particular we wanted to i) assess optimal and suboptimal food sources for development of *H. axyridis* and determine their influence on larval fitness, ii) test whether suboptimal food sources would increase in value for *H. axyridis* larvae by dietary mixing, iii) evaluate the nutritional quality of different floral food sources for development of *H. axyridis* and iv) determine if utilization of different floral food sources differs between larvae and adult *H. axyridis*. We conducted laboratory experiments to investigate the utilization of plant-derived food sources by *H. axyridis* larvae and a semi-field experiment with adults to assess the influence of the floral resources on the adult beetles' energetic budget. The results would help to assess whether flower strips could provide *H. axyridis* with an additional competitive advantage when compared to native

species.

2. Material and methods

2.1. Insect material

Adult *H. axyridis* were collected around Zurich, Switzerland in 2013 and reared in 1.8 L plastic containers to establish a breeding colony. They were fed with eggs of *Ephesia kuehniella* Zeller (Lepidoptera: Pyralidae) (Biotop, Valbonne, France). Egg batches of *H. axyridis* were regularly removed and the hatching larvae were used for the experiments.

Spodoptera littoralis (Boisduval) (Lepidoptera: Noctuidae) (provided as eggs by Syngenta Crop Protection Münchwilen AG, Stein, Switzerland) were reared on *Fagopyrum esculentum* (buckwheat) leaves until they reached a suitable size to be fed to *H. axyridis* (larval stage 1–4 according to the size of *H. axyridis* larvae). *Acyrtosiphon pisum* Harris (Hemiptera: Aphididae) were used from a long term laboratory culture kept at Agroscope on common bean plants (*Vicia faba*) and were fed to *H. axyridis* as mixed stages.

2.2. Plant material

Plants were chosen according to observed positive effects on natural enemies and common presence in flower strips (Tschumi et al., 2016). Seeds (Fenaco Genossenschaft Bern, Switzerland) were either sown into 6 L pots without fertilizer in a greenhouse or directly into the field (semi-field experiment). For laboratory experiments flowers from *F. esculentum*, *Papaver rhoeas* (poppy), *Calendula arvensis* (field marigold), *Sinapis arvensis* (mustard), and *Centaurea cyanus* (cornflower) were grown. Newly opened flowers were cut daily, placed with the stalk into an Eppendorf vial with water and fixed with cotton wool to be used in the experiments. *F. esculentum* and *S. arvensis* flowers both possess a corolla with broad aperture and low to intermediate depth and therefore their nectar and pollen should be well accessible for the ladybirds (Vattala et al., 2006). *Centaurea cyanus* provides easy accessible food due to the presence of extrafloral nectaries, as does *P. rhoeas*, which produces abundant pollen (Bosch et al., 1997). In comparison, *C. arvensis* is a composite with small tubular florets that could be less accessible to the ladybird larvae even though their strong biting mandibles might allow them to reach floral resources by destruction of the flower structure.

Maize plants (*Zea mays* var. Gavott, KWS Saat GmbH, Einbeck, Germany) were grown individually in 12 L plastic pots with 40 g of slow release fertilizer (Osmocote Exact, 16% N, 11% P₂O₅, 11% K₂O, Scotts UK Professional, Bramford, UK). When plants had reached the three leaf stage liquid fertilizer (0.4 L of 0.2% Vegesan standard; Hauert HBG Dünger AG, Grossaffoltern, Switzerland) was added once per week. To collect pollen, air-permeable cellophane bags (19.5 × 37.5 cm, Celloclair AG, Liestal, Switzerland) were clipped over the inflorescences and pollen was collected daily by cutting a small hole into the bottom of each bag. The pollen was passed through a fine mesh (0.2 mm) and dried at room temperature for 1 d before storage in a freezer (−23 °C). Prior to feeding-experiments the pollen was kept for 24 h in a plastic box with saturated humidity.

2.3. Laboratory experiments

The suitability of different food sources for the development and survival of *H. axyridis* larvae was determined in three separate laboratory experiments. The experiments were run in a climate chamber at 24 °C, 75% RH and 16:8h light:dark photoperiodic conditions. The larvae were kept separately in small containers (6 cm dia., 8.5 cm height) and fed *ad libitum* with the respective food source. In addition, a small piece (1.2 × 1.2 cm) of *F. esculentum* leaf (except experiment 3) and a drop of water were added. Larvae were checked daily and their

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