# Feeding on Prey and Plants by Omnivorous Consumers: Performance, Foraging, and the Influence of Resource Distribution

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by

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## Abstract

**Background:** True omnivory, the feeding on both prey and plant resources, is extremely ubiquitous in both natural and managed ecosystems. In particular, many predators of agricultural pests consume also plant-provided foods, such as pollen and nectar. In turn, this could influence the life history and behavior of omnivorous predators in various ways, and consequently alter their efficacy in suppressing pest populations. Feeding on plant foods can allow predators to persist during periods of prey scarcity and can provide nutrients that are missing in prey-only diets. However, plant feeding can also distract predators from prey consumption and consequently hinder pest suppression. If prey and plant resources are complementary, true omnivores would be expected to shift their food preferences and travel frequently between the two resources to maintain a balanced diet. Nonetheless, despite its obvious influence on the efficacy of natural enemies, the study of active shifting between feeding on prey and plant foods has been largely neglected.

In this study I addressed various aspects of prey and plant food mixing and its consequences for pest intake by omnivorous natural enemies. Specifically, the objectives of the study were to: 1) test whether supplementing prey diet with pollen enhances the performance of primarily predacious omnivores, 2) estimate the overall influence of pollen supplements on pest intake, 3) examine the influence of diet history on prey and pollen food preferences, and 4) evaluate the influence of the spatial availability of complementary foods on their consumption by omnivores.

**Methods:** The contribution of pollen supplementation of prey diet was examined in a series of experiments that quantified larval survival and development, and oviposition rate in two model organisms, the ladybeetle species *Coccinella septempunctata* and *Hippodamia variegata*. Experimental results were then incorporated in an individualbased model to assess the overall influence of pollen supplements on pest consumption by these two omnivores. Diet shifting behavior was examined in feeding trials: food preference was tested for the two lady beetle species and for *Amblyseius swirskii* mites following diet histories of prey, pollen or prey+pollen. Finally, I developed a spatially explicit individual-based model to explore how the spatial availability of complementary food resources (i.e., plant material and prey) influence

food consumption. Model predictions were then tested empirically in a feeding trial experiment, using *H. variegata* as a model organism.

**Results:** *C. septempunctata* and *H. variegata* were unable to complete development or oviposit when fed canola pollen alone. Yet when pollen was provided as a supplement to prey diets, *C. septempunctata* oviposition increased by 1.6 fold and *H. variegata* larval survival increased from 50% to 80%. Therefore, population growth rate of both species would be higher in the presence of canola pollen. However, feeding on pollen could reduce per capita prey intake. Results of the theoretical model, which assessed the total influence of pollen supplements on pest consumption, showed that under certain conditions the positive influence on natural enemy population growth was not sufficient to overcome per capita reduction in pest intake. Diet history had an opposite effect on food preference of mites compared to lady beetle larvae. *A. swirskii* exhibited fidelity to its previous diet, whether prey or pollen. In contrast, *C. septempunctata* larvae shifted their preference asymmetrically; beetles with prey diet history allocated more time to pollen, but not vice versa. Finally, diet history had no significant effect on subsequent food choice by *H. variegata* larvae.
In the spatially explicit individual-based model, prey intake by omnivores was highest when it was situated near complementary plant food resources and when both prey and plant foods were distributed randomly, rather than clustered in the habitat. Moreover, plant spatial availability had a stronger influence on prey intake by zoophytophagous than phytozoophagous consumers. When tested empirically, prey intake of *H. variegata* was not influenced by proximity of prey to pollen resources.

**Conclusions:** The large contribution of a mixed prey and canola pollen diet to the performance of *C. septempunctata* and *H. variegata* supports the notion that plantprovided food supplements act not only as an alternative food when prey is scarce, but also as an essential supplement to prey-only diets. This finding is novel for the two studied species, which until now were considered primarily predacious. Even so, the contribution of pollen supplements to natural enemy population growth must be weighed against their negative effect on per capita prey intake. Heuristic models that assess the total contribution of pollen supplements to pest consumption, such as the one presented in this study, could be used to determine the optimal time and duration of plant food supplementation in particular cropping systems.

Differences in the performance on prey versus pollen diets, may help explain the dissimilar feeding choices made by *A. swirskii* mites and the two lady beetle species. In contrast to the latter, *A. swirskii* is able to complete its life cycle either on pollen or prey alone. Therefore, the physiological and behavioral costs entailed in shifting between such different resources perhaps outweigh the nutritional benefit of a mixed diet in this species. Whether individuals remain loyal to familiar food or shift to complementary resources, the influence of diet history on subsequent feeding choice could be used to enhance biological pest control by providing pre-release diets that subsequently cause natural enemies to feed more on pest items. Results of the spatially explicit individual-based model suggest that for natural enemies that treat prey and plant foods as complementary food sources, plant food supplements would promote the suppression of pest populations best when they are randomly distributed and within close proximity to pest infestation sites. Apart from using the model to optimize the spatial pattern at which plant food supplements are provided, the modeled system broadens our understanding of omnivore foraging and feeding choices in complex environments with multiple food types of various nutritional value.