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Assessing the trophic ecology of the Coccinellidae: Their roles as predators and as prey

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ABSTRACT

Coccinellidae function in complex food webs as predators, as consumers of non-prey foods, and as prey or hosts of natural enemies. Dietary breadth and its implications remain largely unexplored. Likewise the nature and implications of interactions with other predators in the field are poorly understood. The use of biochemical tools based on nucleic acids, proteins, sugars and other components of coccinellid diets, expands our understanding of their trophic ecology – but only under field conditions in which coccinellids live, reproduce, forage, and consume prey (including intraguild prey), pollen, fungi, nectars, and other foods. We review the various methods which have been applied to the study of trophic relationships involving the Coccinellidae, their advantages and disadvantages, and some salient innovations and results produced by the range of technologies and their combinations. We advocate employing multiple tools to generate a more complete picture of the trophic ecology of a predator. The false perceptions of the strength and direction of trophic linkages that can result from a methodologically narrow approach are well illustrated by the laboratory and field assessments of coccinellids as intraguild predators, a phenomenon that is discussed in detail here. Assessing intraguild predation, and the breadth of prey and non-prey foods of the Coccinellidae, is essential to the understanding of this group, and for their application as biological control agents.

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1. Trophic roles of Coccinellidae

Entomophagous coccinellids are major consumers of prey, but are themselves prey for intraguild predators. The processes of finding food and avoiding predation ultimately shape many of the behaviors of lady beetles and the ecological services they provide. Our current knowledge of the dietary breadth of coccinellids is incomplete; it also arises from a variety of approaches and tools used to examine trophic linkages. Likewise, assessments of the strength and outcome of intraguild interactions among coccinellids and other natural enemies are imperfect, and can vary depending on the experimental or observational approaches that are employed.

Coccinellid feeding behavior is much more complex than the stereotype of the aphid-eating lady beetle would suggest. This is not to say that aphidophagous species are unimportant; their conservation and augmentation within cropland can help suppress aphid outbreaks (van Emden and Harrington, 2007; Lundgren, 2009b; Obrycki et al., 2009). But the family Coccinellidae evolved from coccidophagous ancestors, and much of the extant diversity in the family still specializes on this prey group (Giorgi et al., 2009; Hodek and Honěk, 2009). Certain clades have also come to specialize on aleyrodids (Hodek and Honěk, 2009), mites (Biddinger et al., 2009), fungi (Sutherland and Parrella, 2009), plant foliage (Hodek and Honěk, 1996; Giorgi et al., 2009), and even pollen (Hodek and Honěk, 1996). Alternative foods such as lepidopteran and coleopteran immatures (Evans, 2009) and non-prey foods (Lundgren, 2009a) are critical components of optimal diets in most coccinellids, and shape the natural histories of these and other predators (Lundgren, 2009b). As a group, coccinellids are extremely polyphagous; and it is increasingly apparent that species and individuals are in many instances quite polyphagous as well. The simple fact is that there is not a single species for which the entire dietary breadth is known.

The abundance, dispersion, and pest management benefits of coccinellids are influenced by their suite of natural enemies. Parasitoids, parasites (mites) and pathogens (nematodes, viruses, protozoa, bacteria, and fungi) are widespread in many coccinellid populations (Riddick et al., 2009), and their geographic and host ranges have expanded with the anthropogenic redistribution of coccinellids used in biological control. Perhaps equally important are intraguild predators (including other coccinellids) that regularly consume coccinellid eggs (Harwood et al., 2009) and larvae

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(Lucas, 2005; Pell et al., 2008), and ants that defend herbivorous prey from coccinellid predation (Majerus et al., 2007). Pressure from intraguild competitors and other natural enemies drives coccinellid spatio-temporal distributions on many scales, as well as their predation capacity, defensive characteristics, and reproductive decisions (Seagraves, 2009). These intraguild interactions notwithstanding, coccinellids and other natural enemies are now well recognized as operating additively or synergistically in pest suppression (Snyder, 2009).

Research on coccinellids has advanced mankind's concepts of pest management, the nutritional physiology of insects, and how insects function within complex food webs. However, the complex nature of coccinellid trophic ecology must be appreciated and accommodated for their pest management benefits to be fully realized. Specifically, the dietary breadth of coccinellids can only be fully evaluated using multiple diagnostic methods that account for the polyphagous tendencies of these predators in both space and time. This point is well illustrated by the recent scientific attention devoted to intraguild interactions involving coccinellids, discussed in Section 2. The wide breadth of tools currently applied to assess the diets of predators (and coccinellids in particular) can help to resolve (1) the relative contributions of different foods to the nutritional ecology of coccinellids, and (2) the influence of intraguild predation (IGP) interactions on natural enemy communities comprised in part of coccinellids.

2. Caveats for dietary assessments of predators in the laboratory: A case study involving IGP and coccinellids

The importance of using multiple techniques to evaluate the strength of trophic interactions by natural enemies is well illustrated by the staggering number of studies recently published on the relative capability of lady beetles as intraguild predators in relation to other natural enemies. These studies have identified that intrinsic characteristics of predator guilds (including size, chemical and physical defenses, mandibular features, dietary breadth, mobility, degree of satiation, etc.) influence which predator will emerge successful from an intraguild encounter. Among natural enemies, coccinellids are comparatively large-bodied, aggressive, and well defended against predation; all of these traits make lady beetles frequent victors in IGP contests. But evidence from larger scale experiments suggest that the consistently strong trophic relationships between coccinellids and IGP competitors measured in the laboratory are unrealistic. Ultimately, this lends credence to our argument that multiple field-based assessment procedures are necessary to define the role of coccinellids in IGP, and the trophic ecology of the group in general.

2.1. IGP contests with non-coccinellid natural enemies

A number of natural enemies suffer asymmetrically from IGP by coccinellids. Within confined conditions, anthocorids (Santi and Maini, 2006) and predaceous Diptera larvae (Lucas et al., 1998; Gardiner and Landis, 2007) usually lose IGP contests with coccinellids. Parasitoid immatures within parasitized hosts are particularly vulnerable to predation (Snyder et al., 2004; Zang and Liu, 2007; Pell et al., 2008). Coccinellids seldom discriminate between parasitized and unparasitized prey (Colfer and Rosenheim, 2001; Bilu and Coll, 2007; Zang and Liu, 2007; Royer et al., 2008), depending on the age of the parasitoid (e.g., parasitoid pupae or mummies are sometimes less preferred than developing endoparasitoids) (Chong and Oetting, 2007; Zang and Liu, 2007; Hodek and Honěk, 2009). Entomopathogens residing in infected prey are also consumed by coccinellids, and thus these pathogens' ability to suppress a pest population may be reduced by IGP (Pell et al., 2008; Roy et al., 2008). However, even when coccinellids are successful intraguild predators, heterospecific intraguild prey are often poor quality for coccinellids relative to their preferred prey (Phoofolo and Obrycki, 1998; Santi and Maini, 2006; Royer et al., 2008), and IGP is often reduced when alternative prey becomes available (De Clercq et al., 2003; Yasuda et al., 2004; Cottrell, 2005).

Although coccinellids are often successful intraguild predators, they also are victims of IGP. Ants that tend hemipterans are particularly hostile toward foraging coccinellid adults and larvae, although the intensity of these interactions depends on the species involved (Majerus et al., 2007). Adult coccinellids are usually chased away by ants, and larvae are moved away from the prey colony, pushed off of the plant, or killed (Majerus et al., 2007). Pentatomids also overcome coccinellid immatures in intraguild contests in the laboratory (Mallampalli et al., 2002; De Clercq et al., 2003; Pell et al., 2008). Lacewing larvae (chrysopids and hemerobiids) fare well in IGP contests against coccinellids of similar or smaller size (Lucas et al., 1998; Michaud and Grant, 2003; Santi and Maini, 2006; Gardiner and Landis, 2007). Finally, entomopathogens may also harm the intraguild predators that eat infected prey; aphids infected with the entomopathogen *Neozygites fresenii* (Nowakowski) (Entomophthorales: Neozygitaceae) increased mortality, prolonged development, and reduced fitness of *Coccinella septempunctata* L. versus individuals fed healthy prey (Simelane et al., 2008).

2.2. IGP contests with other coccinellids

Coccinellid species vary greatly in their competitiveness in IGP conflicts. Among coccinellid life stages, eggs are particularly vulnerable to predation, and coccinellids are behaviorally adapted to reduce egg predation from heterospecifics (Seagraves, 2009). In addition to predator avoidance strategies by ovipositing females (Griffen and Yeargan, 2002; Seagraves and Yeargan, 2006; Seagraves, 2009), the chemical defenses present in or on coccinellid eggs partially determine their acceptability to heterospecific predators (Sato and Dixon, 2004; Cottrell 2005, 2007; Pell et al., 2008; Ware et al., 2008); perhaps immunity to the chemical defenses of conspecific eggs is why these are such a suitable food for many coccinellids (Burgio et al., 2002; Sato and Dixon, 2004). Larvae are defended from predation by heterospecific coccinellids through their chemistry, behavior and mobility, and their physical characteristics (e.g., exterior spines or waxy secretions). Like heterospecific coccinellid IGP, cannibalism is also a common phenomenon in coccinellids, but differs in important nutritional, selective, and evolutionary implications (Osawa, 2002; Michaud, 2003; Michaud and Grant, 2004; Omkar et al., 2006; Seagraves, 2009).

2.3. Implications of IGP for biological control

Nearly all the studies in Sections 2.1 and 2.2 assess the relative ability of a coccinellid species to function as an intraguild predator of a conspecific or heterospecific natural enemy within confined experimental conditions (either a Petri dish or a "microcosm"). For example, 73% of the 30 studies on IGP involving coccinellids reviewed by Lucas (2005) were conducted in the laboratory, and 10% were conducted in field cages. These experiments are valuable in assessing the propensity of one species to successfully attack another, all else being equal. But under field conditions, habitat characteristics (e.g., three-dimensional complexity and refugia), availability of alternative food sources, activity cycles of the participants, and avoidance and escape behaviors of potential intraguild prey strongly influence the outcome of these interactions (Lucas, 2005; Majerus et al., 2007; Pell et al., 2008). Also, much of the research to date has focused on interactions in cropland, and the influence of IGP by and on coccinellids in natural systems remains to be substantiated (Pell et al., 2008). Field observations of IGP