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Omnivores as plant bodyguards—A model of the importance of plant quality

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Abstract

The importance of omnivores in ecological systems is increasingly being recognized, not least due to their intensified use as biocontrol agents in crop production. We model a simple plant–herbivore–omnivore (predator) system to explore the effects of plant suitability as food for omnivores on the outcome of omnivore–herbivore interactions. The model predicts that increasing plant suitability relative to herbivore suitability for the omnivore will catalyze the extinction of herbivores or omnivores, depending on the relative growth rate of omnivores feeding solely on plants or herbivores. When omnivore growth is higher on plants, either the omnivore or the herbivore goes extinct. When omnivore growth is higher on herbivores, the possible consequences are extinction, stable coexistence, and limit cycles, depending on the combination of species properties. Our results suggest that plants in some situations may evolve towards becoming more suitable to omnivores to escape detrimental herbivores and that breeders could manipulate crop suitability to omnivore species to reach a desired outcome of omnivore–herbivore interactions.

Zusammenfassung

Die Bedeutung von Omnivoren in ökologischen Systemen findet zunehmende Beachtung, nicht zuletzt wegen der verstärkten Nutzung als natürliche Feinde von Schädlingen in der Landwirtschaft. Wir formulierten ein einfaches Pflanze-Herbivor-Omnivor(Räuber)-System, um den Einfluss der Eignung der Pflanze als Nahrung für Omnivoren auf das Ergebnis von Omnivoren-Herbivoren-Interaktionen zu erkunden. Das Modell sagt voraus, dass zunehmende Eignung der Pflanze für den Omnivoren relativ zur Eignung des Herbivoren das Aussterben des Herbivoren oder des Omnivoren bewirken wird, abhängig von der Wachstumsrate des Omnivoren, wenn er nur Pflanzen bzw. Herbivoren frisst. Wenn das Wachstum des Omnivoren bei pflanzlicher Nahrung höher ist, sterben entweder der Omnivore oder der Herbivore aus. Wenn das Wachstum des Omnivoren bei tierischer Kost größer ist, sind die möglichen Folgen Aussterben, stabile Koexistenz oder Grenzzyklen, jeweils in Abhängigkeit von der Kombination der Eigenschaften der Arten. Unsere Ergebnisse legen nahe, dass sich Pflanzen in bestimmten Situationen so entwickeln könnten, dass sie für den Omnivoren geeigneter werden, um so schädliche Herbivoren zu vermeiden. Züchter könnten die Eignung von Nutzpflanzen für omnivore Arten so beeinflussen, dass das gewünschte Ergebnis der Omnivoren-Herbivoren-Interaktionen erreicht wird.

Keywords: Intraguild predation; Herbivory; Omnivory; Biological control; Plant quality; Omnivore diet; Tri-trophic interactions; Food webs; Integrated pest management; Host plant resistance

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Introduction

Omnivores have double roles in ecosystems, being able to consume both plant food and animal food as their primary food source (Lundgren 2009; Wäckers, van Rijn, & Bruin 2005). This duality implies that they can impose positive effects on host plants by consuming detrimental herbivores (van den Meiracker & Ramakers 1991), but also impose negative effects by consuming plant biomass (Trottin-Caudal, Fournier, Leyre, & Chabriere 2006). In this paper, we will specifically consider under what circumstances omnivores can be used to control herbivores rather than act as plant enemies.

Though arriving from partially different traditions, both basic and applied researchers are now increasingly becoming aware that plant quality as food for omnivores is critical for the outcome of omnivore–herbivore interactions. From a basic ecology perspective the role of omnivores has mainly been explored with respect to their effect on food web stability. In a seminal paper, Holt and Polis (1997) identified some of these characteristic features of intra-guild predation (IGP): (i) coexistence requires that the herbivore is superior competitor for the plant and the omnivore gains significantly from consuming the herbivore; (ii) coexistence should be most likely at intermediate resource levels; (iii) alternative stable states exist.

Studies specifically directed at plant–herbivore–omnivore interactions by Coll and Izraylevich (1997) and Namba, Tanabe, and Maeda (2008) showed that increased plant consumption by the omnivore can decrease stability and bring about chaos in the system, while Lalonde, McGregor, Gillespie, and Roitberg (1999) showed that density-dependent plant feeding by omnivores may increase stability. In addition several studies have shown that plant food and animal food have different effects on omnivore performance and growth; in some cases these resources are nutritionally complementary, but in other cases substitutable (Berkvens et al. 2008; De Clercq, Bonte, Van Speybroeck, Bolckmans, & Deforce 2005; Vantornhout, Minnaert, Tirry, & De Clercq 2004), which may have implications for stability and coexistence, and hence plant damage.

From a more applied ecology perspective, omnivores, being important enemies of many pest herbivores, have lately received much interest as biocontrol agents (Lundgren 2009; Stenberg, Lehrman, & Björkman 2010). The advantage of omnivorous predators, in comparison with pure carnivores, is that they can utilize plant food during periods of herbivore scarcity, rarely leaving the stage to let herbivorous prey enjoy enemy-free space. Because most omnivores only cause minor quantitative damage when feeding on plant photosynthetic tissues in comparison to herbivore pests, they are engaged in agriculture as so-called plant "bodyguards". However, although highly promising, the outcome of putting omnivores into action in agriculture has varied widely from successes with herbivore reduction to failures with plant-feeding omnivores only worsening crop damage. Consequently, the same omnivore species have in some papers been suggested as useful biocontrol agents (e.g. van den Meiracker & Ramakers 1991) and in others as pest insects (e.g. Trottin-Caudal et al. 2006). Recently it has been suggested that differential host-plant quality may be responsible for the different outcomes (Coll 2009; Eubanks & Denno 2000). As host-plant quality is known to vary much more within and among plant species than animal food quality, the relative quality difference between plant food and animal food for omnivores is highly dependent on plant quality.

A growing body of empirical studies has recently provided evidence for the importance of plant quality for the outcome of omnivore–herbivore interactions (Coll 1996; Lundgren 2009; Lundgren, Hesler, Tilmon, Dashiell, & Scott 2009; Magalhães, Janssen, Montserrat, & Sabelis 2005; Mahdian, Tirry, & De Clercq 2007; Stenberg, Lehrman, & Björkman 2011). Although individual studies point in different directions, some evidence suggests that in the short run increased host plant quality may partly release herbivores from omnivore predation (Agrawal, Kobayashi, & Thaler 1999; Stenberg et al. 2011), while in a longer perspective, high quality plants may support higher omnivore densities, which eventually cause stronger negative impacts on the herbivores (Eubanks & Denno 2000).

Given that omnivore feeding is less detrimental than herbivore feeding on plants (see e.g. Björkman, Höglund, Eklund, & Larsson 2000; Lauenstein 1979) one should presume that plant genotypes that catalyze herbivore removal by predacious omnivores should be favored by natural selection. Likewise, knowledge of which plant qualities that mediates herbivore removal by less damaging omnivorous herbivores would be very valuable for crop breeders in order to develop less susceptible varieties. Thus, progress in understanding how plant quality affects the outcome of omnivore–herbivore interactions will help us understand the evolution of plants in relation to herbivore selection, and spur new advances in crop breeding.

Experiments deliberately intended to investigate long-term interactions between omnivores and herbivores are almost non-existent. Due to the current lack of good long-term studies it is presently not possible to generalize from observations. A useful alternative approach to better understand factors underlying stable persistence and replacement in omnivore–herbivore interactions is modeling. We consider a commonly found system, principally consisting of one host plant, one herbivore feeding on the plant, and one true omnivore, which may consume the herbivores or the host plant depending on their relative supply. Previous models (Coll & Izraylevich 1997; Lalonde et al. 1999; Namba et al. 2008) of systems of this type have mostly focused on the conditions under which such tri-trophic systems become chaotic. We will here focus on the omnivore–herbivore interaction and investigate under which circumstances plant quality will lead to the exclusion of the herbivore, exclusion of the omnivore, or coexistence.