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How functional response and productivity modulate intraguild predation

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Abstract. Numerous models have been developed to predict the effect of environmental productivity on the coexistence of prey and predators within the three-species module of intraguild predation. Theoretical models have mainly used Holling Type I and Type II functional response, the latter typically best describing the functional response of a predator. However, no empirical study has simultaneously examined the form of the functional response and the effect of prey density on intraguild interactions. This is surprising considering that the strength of the functional response is crucially important for the stability of simple predator-prey systems and the persistence, sustainability and biodiversity of communities. In this study, we first developed a linear and a nonlinear functional response model for intraguild predators and next used a plant–aphid–predator mesocosm to parameterize the models and test their predictions at different prey densities. As expected, the assumptions of the linear model are not supported by empirical results which lead to systemic overestimation of the predation rate and the intensity of intraguild predation. On the other hand, the predictions of the nonlinear functional response model fit very well with experimental observations mainly because key behavioral characteristics such as handling time are integrated in this model. The nonlinear model is thus a good predictor of intraguild predation and allows a better understanding of how environmental productivity and predator behavior influence the occurrence and outcome of multiple predator interactions.

Key words: *Aphidoletes aphidimyza*; *Coleomegilla maculata*; food web; insects; mesocosm experiment; *Myzus persicae*; predator–prey interactions; prey density.

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INTRODUCTION

Intraguild predation (IGP), a special case of multiple predator interaction, occurs when two predator species compete for a common resource and also feed on each other (Polis et al. 1989). IGP is a widespread interaction in natural and managed ecosystems (Arim and Marquet 2004) that may influence the structure and dynamics of communities (Holt and Polis 1997, Morin 1999, Mylius et al. 2001, Vance-Chalcraft et al. 2007) and, from an applied perspective, the outcome of biological control and the management of endangered or exotic invasive species (Rosenheim et al. 1995, Rosenheim 1998, Müller and Brodeur 2002, Vance-Chalcraft et al. 2007, Straub et al. 2008). Following the publication of a general theory of IGP by Holt and Polis (1997), several models and empirical studies have investigated the nature and prevalence of IGP in diverse terrestrial and aquatic communities. An important component of this theory is the effect of environmental productivity on the coexistence of competing organisms (Holt and Polis 1997, Morin 1999, Diehl and Feissel 2000, 2001, Mylius et al. 2001, Borer et al. 2003). According to the theory, only the intermediate predator (i.e., the intraguild prey; IG prey) should persist at low productivity because it has a better capacity to exploit resources than the top predator (i.e., the intraguild predator; IG predator), whereas the latter should drive the IG prey to extinction at high productivity through a combined effect of competition and predation. Therefore, IGP theory predicts that coexistence can only occur at intermediate productivity levels (Holt and Polis 1997, Diehl and Feissel 2000, Mylius et al. 2001, Borer et al. 2003, Borer et al. 2007), but few empirical studies have validated this prediction (Diehl and Feissel 2000, 2001). In contrast to the theory, many field and laboratory experiments have reported cases of coexistence over a large gradient of productivity (Lawler and Morin 1993, Morin 1999, Amarasekare 2000, Borer et al. 2003, Amarasekare 2007, 2008, Lucas and Rosenheim 2011). Moreover, IGP generally tends to decrease as the density of the shared or extraguild (EG) prey increases (Lucas and Rosenheim 2011), suggesting that at high productivity (typically characterized by high EG prey density) IGP may not be common and coexistence possible.

The mismatch between model predictions and empirical observations suggests that models do not correctly translate some important features of trophic and guild interactions occurring in food webs. According to several authors, a careful examination of predator and prey behaviors may help to deepen our understanding of multiple predator interactions and improve theoretical models (Sih et al. 1998, Rosenheim and Corbett 2003, Schmitz 2007, Steffan and Snyder 2010). For instance, McCoy et al. (2012) recently reported that characterizing the predators' functional responses would improve model predictions about the combined effects of multiple predators on prey survival. Similarly, Lucas and Rosenheim (2011) hypothesized that the shape of the predators' functional response contributes to explain why IGP is less frequent when EG prey density increases. Most interestingly, theoretical model predictions differ depending on the type of functional response: IGP models assuming a linear functional response for the IG predator lead to predictions of high extinction probability of the IG prey under conditions of high productivity (Holt and Polis 1997, Diehl and Feissel 2000, Borer et al. 2003, Briggs and Borer 2005, Borer et al. 2007, Hall 2011) whereas, with nonlinear functional response models, predation rate reaches a maximum at high prey densities resulting in a weaker interaction that could decrease IGP intensity and thereby the probability of IG prey extinction (McCann and Hastings 1997, McCann et al. 1998, Uchida et al. 2007, Rall et al. 2008, Williams 2008, Abrams and Fung 2010). Therefore, testing assumptions of theoretical models and evaluating differences between the linear and nonlinear functional response models is crucial for improving these models and deepening our understanding of multiple predator interactions across a productivity gradient. However, although most functional responses are known to be of type II or type III in multi-prey systems, no empirical study has examined to our knowledge which functional response model best describes the behavior and predation rate of an IG predator along a productivity gradient. This is perplexing given the critical role of functional response and thereby interaction strength for community dynamics and ecosystem functioning.

In this study, we experimentally compare predictions of the linear and nonlinear functional response models examining IG interactions across a gradient of extraguild prey density. We first developed both models for general IG interactions and next used a plant–aphid–predator mesocosm to parameterize models and generate specific predictions. Next, we tested model predictions by manipulating aphid density within our experimental system. Finally, we quantitatively tested the empirical intuition of Lucas and Rosenheim (2011) following which the effect of the EG prey density on the occurrence of IGP depends on the benefits/costs of eating the IG prey and on the handling capacity of the IG predator, which are related to the search rate and handling time parameters of the functional response model, respectively.

Models

The nonlinear model

Most functional response models are based on the Holling Type II equation (1959), also known as the disc equation, because it adequately describes the behavior of the vast majority of predators (Jeschke et al. 2002). However, this model becomes invalid when a predator removes a substantial proportion of prey that are not replaced, which is a common feature of functional response (Juliano 2001) and multiple predator experiments (McCoy et al. 2012). In such a case, a modification of the disc equation proposed by Rogers (Rogers 1972), and known as the random predator equation, should be used:

$$N_e = N_0 \times \left(1 - e^{-a(t - hN_e)}\right) \tag{1}$$

where N_e is the number of prey eaten, N_0 the initial density of prey (units: prey area^{-1}), t the total experimental time, a the search rate (searching efficiency of the predator; units: area time^{-1}), and h the handling time (time to attack, kill, and eat a prey; units: time prey^{-1}). The reciprocal value of the handling time parameter corresponds to the maximum feeding rate, which is approached asymptotically as prey density increases.

Adding an IG prey to a simple prey–predator food chain can affect the number of extraguild prey eaten by the IG predator in a number of ways. For instance, the pursuit, capture, and consumption of IG prey reduce the amount of time available for encountering EG, prey and vice versa. This effect can be included in the basic Type II functional response (Eq. 1) as follows (Lawton et al. 1974):

$$N_{eg} = N_{0eg} \times \left(1 - e^{-a_{eg}(t - h_{eg}N_{eg} - h_{ig}N_{ig})}\right) \tag{2}$$

$$N_{ig} = N_{0ig} \times \left(1 - e^{-a_{ig}(t - h_{ig}N_{ig} - h_{eg}N_{eg})}\right) \tag{3}$$

where the subscripts refer to the two prey types: *eg* (extraguild) and *ig* (intraguild). N_{eg} and N_{ig} are the number of EG and IG prey eaten by the IG predator, respectively.

The total number of prey eaten by the IG predator is:

$$\begin{aligned} N_{eg} + N_{ig} = {} & N_{0eg} \times \left(1 - e^{-a_{eg}(t - h_{eg}N_{eg} - h_{ig}N_{ig})}\right) \\ & + N_{0ig} \times \left(1 - e^{-a_{ig}(t - h_{ig}N_{ig} - h_{eg}N_{eg})}\right). \end{aligned} \tag{4}$$

In this model, the IG predator can feed on both the EG prey (with attack rate a_{eg}) and the IG prey (with attack rate a_{ig}). The difference between the search rates determines the preference of the IG predator for one of the prey types (if $a_{eg} > a_{ig}$ then the IG predator prefers the EG prey and vice versa). Note that search rates are independent of prey density, which means that predators do not switch from one prey to the other.

The linear model

In linear functional response models, the only difference with the nonlinear model is that the predator spends all its time searching for prey (i.e., handling time is assumed to be null). Setting the handling time value as null in Eqs. 2 and 3 yields:

$$N_{eg} = N_{0eg} \times (1 - e^{-a_{eg}t}) \tag{5}$$

$$N_{ig} = N_{0ig} \times (1 - e^{-a_{ig}t}). \tag{6}$$

Then, the total number of prey eaten by the IG predator is:

$$\begin{aligned} N_{eg} + N_{ig} = {} & N_{0eg} \times (1 - e^{-a_{eg}t}) \\ & + N_{0ig} \times (1 - e^{-a_{ig}t}). \end{aligned} \tag{7}$$

Following Eq. 7, the total number of prey eaten by the IG predator ($N_{eg} + N_{ig}$) increases linearly with prey densities (N_{0eg} and N_{0ig}).

In the next section, we adapt these two general models to our biological system. Because the general and specific model predictions are similar, we only detailed one of them below.

Application of the Two Models to Aphid Predators

Ubiquitous and abundant in a majority of terrestrial ecosystems, aphids are among the most important pests of temperate agricultural zones (Van Emden and Harrington 2007). Their colonies rapidly grow and decrease, and are exploited by a large number of predator, parasitoid and pathogen species (Dixon 1977, Völkl et al. 2007).

Because most species of predators and parasitoids numerically respond to aphid density and tend to aggregate in densely populated patches (Turchin and Kareiva 1989, Chacón and Heimpel 2010), aphids and the guild of their consumers constitute excellent models to explore food web interactions, including IGP, a very common interaction among aphidophagous predators and parasitoids (Brodeur and Rosenheim 2000, Lucas 2005, Gagnon et al. 2011). In the present study, under laboratory conditions, we studied interactions between the green peach aphid *Myzus persicae* Sulzer (Homoptera: Aphididae, the extraguild prey), the spotted ladybeetle *Coleomegilla maculata lengi* Timberlake (Coleoptera: Coccinellidae, the intraguild predator), and the predatory midge *Aphidoletes aphidimyza* Rondani (Diptera: Cecidomyiidae, the intraguild prey). The ladybeetle is a generalist predator that actively searches for prey while the larva of the predatory midge specializes on aphids and is a furtive hunter that does not trigger prey defensive response (Lucas and Brodeur 2001). IGP is asymmetric as *A. aphidimyza* cannot feed on *C. maculata* (Lucas et al. 1998). These three insect species have overlapping niches and may coexist in nature (Boiteau 1983).

As *Aphidoletes aphidimyza* larvae live within the aphid colony and move slowly, we assumed a similar search rate for *C. maculata* exploiting either intra- or extraguild prey (i.e., $a_{eg} = a_{ig}$), a situation corresponding to an opportunistic IGP type (i.e., IGP is a fortuitous event, Lucas 2005).

The nonlinear model

Setting $a_{eg} = a_{ig}$ in Eq. 4 yields to:

$$N_{eg} + N_{ig} = (N_{0eg} + N_{0ig}) \times \left(1 - e^{-a_{eg}(t - h_{eg}N_{eg} - h_{ig}N_{ig})}\right). \tag{8}$$

Using the Lambert W function (Corless et al. 1996, McCoy and Bolker 2008) to solve this recursive function of N_{eg} and N_{ig} yields to (see Appendix and Bolker 2008 for details):

$$N_{eg} + N_{ig} = (N_{0eg} + N_{0ig}) \times \left(1 - \frac{w\left(a_{eg}(h_{eg}N_{0eg} + h_{ig}N_{0ig}) \times e^{-a_{eg}(t - h_{eg}N_{0eg} - h_{ig}N_{0ig})}\right)}{a_{eg}(h_{ig}N_{0ig} + h_{eg}N_{0eg})}\right). \tag{9}$$

For the number of IG prey eaten, assuming a similar search rate for *C. maculata* when exploiting IG or EG prey in Eq. 3, yields:

$$N_{ig} = N_{0ig} \times \left(1 - e^{-a_{eg}(t - h_{ig}N_{ig} - h_{eg}N_{eg})}\right). \tag{10}$$

Using the Lambert W function (Corless et al. 1996, McCoy and Bolker 2008) to solve this recursive function of N_{eg} and N_{ig} yields to (see Appendix and Bolker 2008 for details):

$$N_{ig} = N_{0ig} \times \left(1 - \frac{w\left(a_{eg}(h_{eg}N_{0eg} + h_{ig}N_{0ig}) \times e^{-a_{eg}(t - h_{eg}N_{0eg} - h_{ig}N_{0ig})}\right)}{a_{eg}(h_{ig}N_{0ig} + h_{eg}N_{0eg})}\right). \tag{11}$$

The linear model

For the total number of IG prey eaten, assuming a similar search rate for *C. maculata* when exploiting IG or EG prey in Eq. 7, yields:

$$N_{eg} + N_{ig} = (N_{0eg} + N_{0ig}) \times (1 - e^{-a_{eg}t}). \tag{12}$$

Similarly, for the number of IG prey eaten, setting $a_{eg} = a_{ig}$ in Eq. 6 yields:

$$N_{ig} = N_{0ig} \times (1 - e^{-a_{eg}t}). \tag{13}$$

Comparison of the predictions of both models

Because search rate and handling time are assumed constant and null, respectively, the linear model (Eq. 12) predicts that the total number of prey eaten by *C. maculata* increases linearly with *M. persicae* and *A. aphidimyza* densities (Fig. 1A). In contrast, the nonlinear model (Eq. 8) predicts that the total number of prey eaten by *C. maculata* increases with *M. persicae* and *A. aphidimyza* densities but reaches an asymptote at higher prey densities because the predator is limited by the time available for handling prey (Fig. 1B).

Following the linear model prediction (Eq. 13), the number of IG prey eaten only depends on IG predator search rate and IG prey density (Fig. 2A). In contrast, the nonlinear model predicts that the number of IG prey eaten decreases as the density of extraguild prey increases (Fig. 2B and Eq. 10). Note that Eqs. 13 and 10 are similar as N_{eg} and N_{ig} approach the origin:

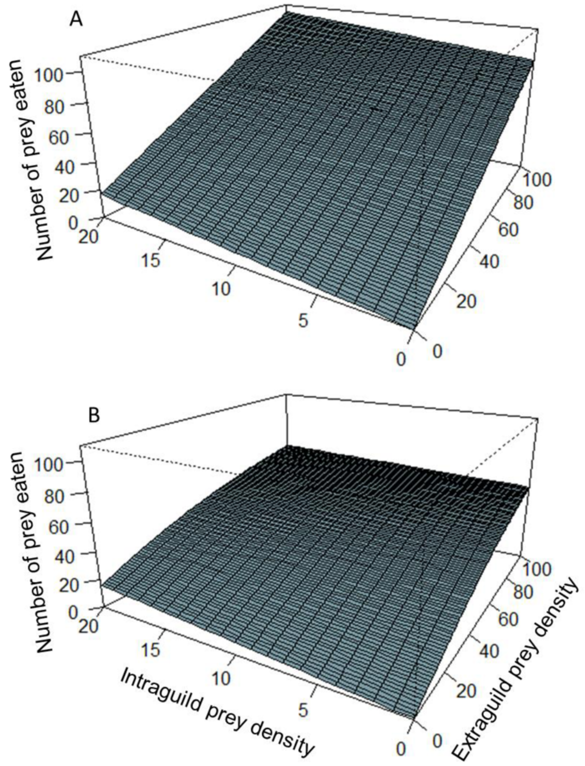

Fig. 1. Total number of prey eaten by an intraguild predator as a function of intra- and extraguild prey densities. (A) Predictions of the linear functional response model derived from Eq. 12. (B) Predictions of the nonlinear functional response model derived from Eq. 8. Parameter values are $t = 1$, $a_{eg} = a_{ig} = 2$, and $h_{eg} = h_{ig} = 0.01$.

$$\lim_{\substack{N_{eg}\to 0\\ N_{ig}\to 0}} \left(1 - e^{-a_{eg}(t - h_{eg}N_{eg} - h_{ig}N_{ig})}\right) = 1 - e^{-a_{eg}t}. \quad (14)$$

In other words, the predictions of both models are similar at low prey densities but diverge more and more as prey densities increase.

Only three parameters are needed to generate model predictions: the search rate for *M. persicae* (a_{eg}) and the handling times for both *M. persicae* (h_{eg}) and *A. aphidimyza* (h_{ig}). Sentis, Hemptinne and Brodeur (2012) estimated mean values (± SE) of a_{eg} as 2.064 ± 0.756 (0.28 m^2 day^{-1}) and h_{eg} as 0.072 ± 0.006 (day prey^{-1}) at 22°C. Note that 0.28 m^2 corresponds to the area of the experimental arena, so 0.28 m^2 day^{-1} is equivalent to arena day^{-1}. The following two experiments were designed to estimate the third parameter, h_{ig} (Experiment 1) and test the predictions (Eqs. 9, 11, 12, and 13) of both models (Experiment 2).

MATERIALS AND METHODS

About 4,000 adult *C. maculata* were collected in October 2009 in a field at Saint-Mathieu-de-Beloeil (45°35′ N, 74°45′ W, Québec, Canada), brought back to the laboratory, and reared in sealed plastic mesh boxes (946 mL) containing moistened paper strips as a source of water. Coccinellids were fed ad libitum with pollen, a liver-based artificial diet (Firlej et al. 2006), and a mixture of three aphid species (*M. persicae*, *Aphis glycines* Matsumura, and *Acyrthosiphon pisum* Harris). For these experiments, a colony of *M. persicae*, established from individuals collected in greenhouses of Agriculture and Agri-Food Canada, St-Jean-sur-Richelieu, Québec, Canada, was

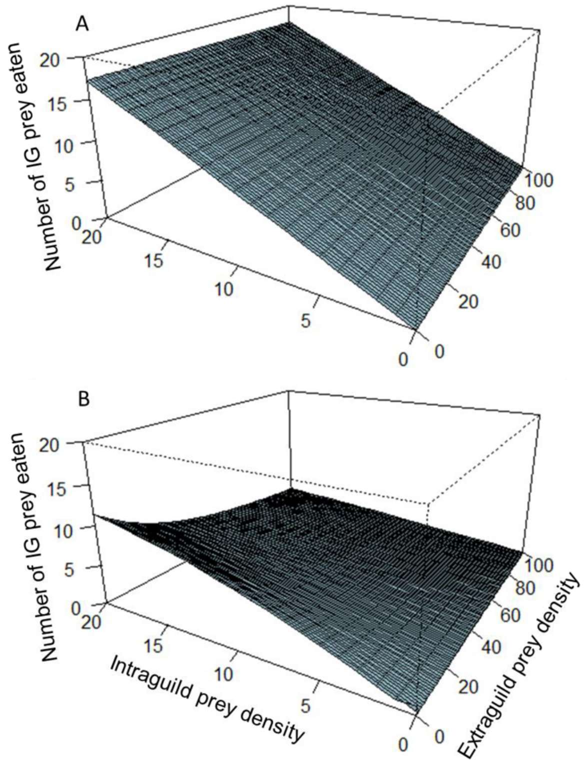

Fig. 2. Number of intraguild prey eaten by an intraguild predator as a function of intra- and extraguild prey densities. (A) Predictions of the linear functional response model derived from Eq. 13. (B) Predictions of the nonlinear functional response models derived from Eq. 11. Parameter values are $t = 1$, $a_{eg} = 2$, and $h_{eg} = h_{ig} = 0.01$.

maintained on sweet pepper plants (*Capsicum annuum* L. cv. Bell Boy). Pepper plants were fertilized twice a week with a solution of Nitrophoska (12–4–14) with a nitrogen concentration of 100 ppm (Plant-Prod, Montréal, Canada). All insects and plants were reared in a growth chamber (Conviron E15, Controlled Environments, Inc., Winnipeg, Manitoba, Canada) at 24 ± 1°C, 50–60% relative humidity, 150 μmol m^{-2} s^{-1} light intensity, and under a 16L:8D photoperiod. During the experiments, temperature and humidity were recorded continuously using Hobo U12 units (Hobo, Onset Computer Corporation, Inc., Bourne, MA, USA).

Experiment 1:
The handling time for A. aphidimyza (h_{ig})

The first experiment was designed to measure *C. maculata* handling time for *A. aphidimyza* (h_{ig}) by direct observation. The experiment was conducted at 22 ± 1°C and under a relative humidity of 70 ± 8%. After hatching, *C. maculata* larvae were reared at 24°C in Petri dishes (100 × 15 mm) and fed green peach aphids ad libitum until they reached the third instar. The larvae were held in Petri dishes lined with moistened paper filter and starved for 21 h prior to the experiment to standardize their hunger drive. To standardize prey size, *A. aphidimyza* females were allowed to oviposit for 10 h on a pepper plants infested by *M. persicae*. At the end of this period, females were removed and plants kept aside until eggs hatched and larvae reached 1.3 mm in length (on average 72 h after hatching). Predatory midge larvae were then isolated in a Petri dish (40 × 12 mm) lined with a thin layer of agar (1.5% concentration) covered with a disk of pepper leaf (40 × 12 mm). They were allowed to acclimatize to these conditions for 30 minutes. A single *C. maculata* larva was next introduced into the Petri dish, and its activity was recorded using an HD camera (Sony HDR-XR500). If the ladybeetle did not attack a midge larva after 4 h, recording was interrupted. We viewed videotapes to measure handling time, defined as the time interval from the beginning of an attack of *C. maculata* on *A. aphidimyza* to the moment when the ladybeetle finished eating. In all replicates, no attack failed and *C. maculata* never moved away before entirely consuming its prey. There were twelve replicates.

Experiment 2:
Testing model predictions

The second experiment was designed to test predictions of the two functional response models (Eqs. 9, 11, 12, and 13) by recording the total number of prey eaten by a *C. maculata* larva and the frequency of IGP between *C. maculata* and *A. aphidimyza* at different densities of *M. persicae*. The experiment was conducted at 22 ± 1°C, under a relative humidity of 70 ± 8%, and with a photoperiod of 16L:8D. The insects were placed on standardized pepper plants that were individually enclosed in a plastic cylinder (20 cm in diameter and 45 cm in height) glued to a disc platform. The top of the cylinder and the two lateral openings were covered with muslin to allow air circulation. Pepper plants used in experimental arenas had four leaves and were four weeks old. Plant apexes were cut because aphids are difficult to count when hidden in the opening terminal buds. To standardize predators, we used the same rearing and starvation conditions as in Experiment 1. At the onset of the experiment, third instar aphids obtained from synchronous cohorts of *M. persicae* were transferred to the upper leaves of the plants using a fine camel-hair brush. We tested three extraguild prey densities: 10, 45, and 90 *M. persicae* per plant. These represent low, average, and high prey densities for a third instar *C. maculata* larva, since Sentis, Hemptinne and Brodeur (2012) showed that *C. maculata* eats on average 35 *M. persicae* per day under the same experimental conditions. One hour after aphid introduction, one *A. aphidimyza* larva was placed near the aphid colony; 30 minutes later, a newly molted third instar *C. maculata* larva was introduced at the bottom of the stem. After 24 h, the number of *M. persicae* and *A. aphidimyza* killed was recorded. We were able to distinguish aphids eaten by *C. maculata* and *A. aphidimyza* because the latter extract aphid body contents leaving an empty aphid exoskeleton (Lucas et al. 1998). Fifteen replicates of the IGP treatment (*M. persicae* + *A. aphidimyza* + *C. maculata*), five replicates without *C. maculata* (*M. persicae* + *A. aphidimyza*), and four replicates of the control treatment (*M. persicae* only) were tested for each aphid density. When testing model predictions, we assumed that a prediction is valid if empirical observations are within the 95% confidence interval (CI) of the

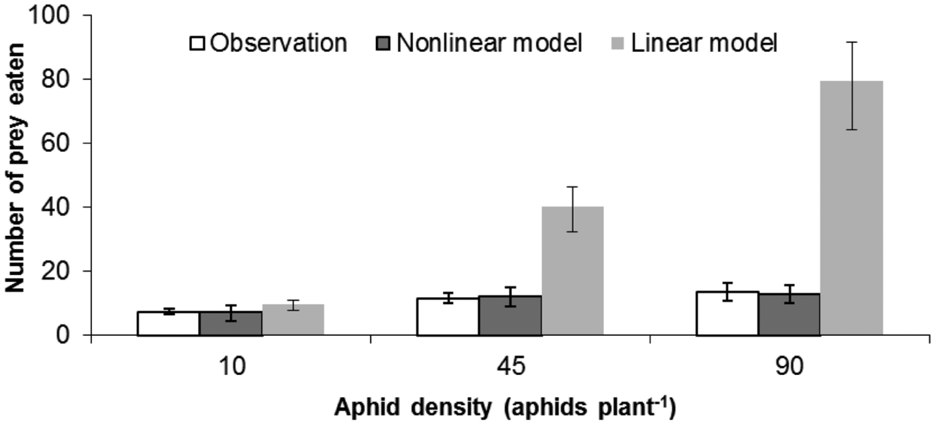

Fig. 3. Empirical observations and predictions of the two models for the total number and 95% CI of prey eaten (*Myzus persicae* + *Aphidoletes aphidimyza*) by *Coleomegilla maculata* as a function of aphid density.

model predictions. Following the law of propagation of uncertainty, which is based on a first-order Taylor series expansion error (Rice 2007), 95% CI of the model predictions were calculated using the standard errors associated with the estimates of each of the model parameters. The package "EMDBOOK" was used to solve the Rogers random predator equation with the Lambert W function (see Appendix and Bolker 2008 for details). Models were developed using R software (version 2.13.1; R Development Core Team 2011).

RESULTS

Experiment 1:
Handling time for A. aphidimyza (h_{ig})

The mean (± SE) handling time for *A. aphidimyza* was 0.0032 ± 0.00034 (day prey^{-1}). This value was included in Eqs. 9, 11, 12, and 13 to generate the predictions of the models.

Experiment 2:
Testing model predictions

Only 0.5 ± 0.1% of the aphids died in the control (no predator). As a result, we did not correct for natural aphid mortality in our analyses. In the treatment without the IG predator (*M. persicae* + *A. aphidimyza*), no *A. aphidimyza* larva died. In the treatment with the IG predator (*M. persicae* + *A. aphidimyza* + *C. maculata*), no *C. maculata* died and IGP was always asymmetric, with *A. aphidimyza* being killed by *C. maculata*.

As predicted by the two models, the total number of prey eaten by *C. maculata* increased with aphid density (Fig. 3). For each aphid density, predictions from the nonlinear model (Eq. 9) fit the empirical observations very well (i.e., were within the 95% CI of the predictions; Fig. 3). Predictions of both models did not differ at the low extraguild prey density (10 aphids per plant). However, the total number of prey eaten predicted by the linear model (Eq. 12) was always higher than the empirical observation, and this difference increased with aphid density (Fig. 3).

As predicted by the nonlinear model, the observed number of *A. aphidimyza* eaten by *C. maculata* decreased as aphid density increased (Fig. 4). Predictions from the nonlinear model (Eq. 11) fit the empirical observations well for densities of 10 and 45 *M. persicae* per plant, but the number of IG prey eaten at the high prey density (90 *M. persicae* per plant) is overestimated. While predictions of both models did not differ at 10 aphids per plant, the linear model prediction (Eq. 13) was higher than the empirical observation for densities of 45 and 90 aphids per plant (Fig. 4).

DISCUSSION

Numerous models explore the conditions for coexistence of IG predators, IG prey, and EG prey (Holt and Polis 1997, Diehl and Feissel 2000, Krivan 2000, Mylius et al. 2001, Holt and Huxel 2007, Rudolf 2007). These models integrate

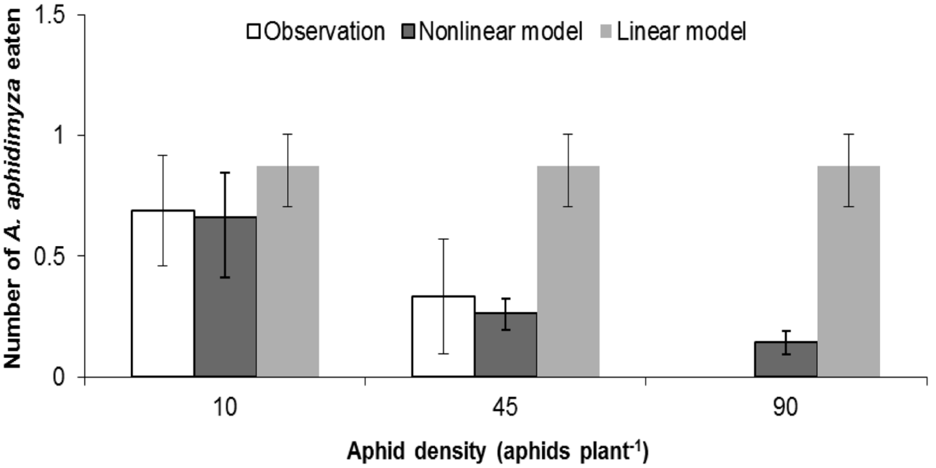

Fig. 4. Empirical observations and predictions of the two models for the number and 95% CI of intraguild prey (*Aphidoletes aphidimyza*) eaten by *Coleomegilla maculata* as a function of aphid (*Myzus persicae*) density. We did not record IGP at 90 aphids plant^{-1}.

different types of functional responses, mainly Holling Type I and Type II. Although most functional responses are known to be of type II in multi-prey systems, no empirical study has examined which type best applies to an IG predator. In this study, we also found that a model based on a linear functional response oversimplifies predator–prey interactions, resulting in predictions that largely deviate from empirical observations. In contrast, the nonlinear model fits our empirical observations well and provides a mechanistic tool that may improve our understanding of important processes underlying IG interactions. Moreover, our study illustrates how the shape of the IG predator functional response contributes to explain the effects of EG prey density on IGP that have been reported in prior studies (see Lucas and Rosenheim 2011 for a review).

We developed both linear and nonlinear functional response models to generate and test predictions about interacting species abundance and IGP intensity. At the low EG prey density, we observed that model predictions were similar and fit the empirical observations well, whereas only the nonlinear model fit the observations at higher EG prey densities (Figs. 3 and 4). However, the nonlinear model overestimated the number of IG prey eaten at the highest experimental EG prey density (Fig. 4). Two non-exclusive factors might explain this result: (1) IGP is a rare event at higher EG prey density and our sampling effort was not sufficient or (2) aspects of the hunting behavior of the IG predator change with prey density, i.e., some form of behavioral prey switching occurs so that *C. maculata* preference for *M. persicae* increases. In this case, our assumption for identical search rates ($a_{eg} = a_{ig}$) might not be true at the highest EG prey density. Functional response parameters depend on several factors (e.g., predator-prey size ratio, morphological and behavioral host defenses, temperature) that typically vary from one experiment to another, and this can be problematic when these parameters are first independently estimated and then used altogether in the same model as we did. Other studies also reported that additive models for combined predator effects cannot account for non-linearity in combined functional response introduced by behavioral interactions between predators and prey (Soluk 1993; see also Colton 1987 for similar conclusions when one predator interacts with two prey species). However, (1) we estimated behavioral parameters and tested model predictions under similar experimental conditions (e.g., growth chamber, temperature, prey size and age), (2) switching generally occurs when eating the IG prey is risky for the IG predator (Lucas 2005); this is not the case for *C. maculata* preying on *A. aphidimyza* larva (Lucas et al. 1998), and (3), in another study (A. Sentis, J. L. Hemptinne and J. Brodeur, *unpublished manu-*

script), we investigated the effect of *M. persicae* density on *A. aphidimyza* intraguild predation along a temperature gradient and concluded that model predictions were well supported by empirical results. Altogether, this suggests that an insufficient sampling effort probably explains the divergence between model predictions and empirical results at the highest EG prey density.

McCoy et al. (2012) recently reported that characterizing the functional response and accounting for prey depletion is important to predict the impact of predator diversity on prey survival. They showed that models based on linear functional response lead to biased predictions and that this bias increases with the level of prey depletion and the degree of nonlinearity of the functional response. Our model also reveals that the magnitude of the bias increases with the value of handling time (i.e., non-linearity). Because *C. maculata* displays a non-linear functional response, (i.e., handling time differs from zero) the linear functional response model overestimated both the number of prey eaten by the predator and the frequency of IGP (Figs. 3 and 4). We also found that the magnitude of the bias increases with initial prey densities (Figs. 3 and 4) mainly because, at low prey density, the predator has to spend much more time searching for than handling prey while, at higher prey densities, the predator is limited by the time available for handling prey. As a result, we conclude that the linear functional response model could be used to predict IGP interactions at high prey densities under specific and uncommon conditions, i.e., when handling or digesting times are negligible. In contrast, the nonlinear model takes into account handling time and therefore generates accurate predictions for most EG prey densities. Our results highlight the importance of accounting for non-linearity in the density dependence of key demographic processes, such as predation rate, to better understand multiple predator interactions. This is critical because most food webs contain many interacting predators and their combined impacts on prey populations remain difficult to predict (Sih et al. 1998, Schmitz 2007, Vance-Chalcraft et al. 2007, Finke and Snyder 2010).

According to prior studies reviewed by Lucas and Rosenheim (2011), the occurrence of IGP usually decreases as extraguild prey density increases. This decrease is generally explained by a prey dilution effect, although the underlying mechanisms remain poorly understood (Lucas and Rosenheim 2011). An analysis of our nonlinear model and experimental results suggests that the dilution effect is linked to both handling time and EG prey density: as EG prey density increases, the time spent killing and consuming EG prey increases, which in turn reduces the time available for encountering IG prey and thereby the frequency of IGP. Therefore, variations in handling time would determine the strength of the dilution effect: the lower the handling time, the larger the number of EG prey needed for the IG prey to benefit from a dilution effect, and vice versa. As a consequence, the linear model is a poor predictor of a dilution effect because handling time is considered null.

In addition to handling time, the reliability of predator–predator models also largely depends on searching (hunting) behavior (Schmitz 2007, Lucas and Rosenheim 2011), which can be characterized by the predator search rate (Rosenheim and Corbett 2003). In functional response models, search rate determines the preference for or the ability to find a particular prey and, for a top predator, the likelihood of IGP. In our experiments, search rates for both prey were assumed similar ($a_{ig} = a_{eg}$), indicating that *C. maculata* behaved like a pure generalist (McCann and Hastings 1997, Borer et al. 2007). However, this might not be the case in other systems where the benefit/cost ratio of eating the IG prey varies. Lucas (2005) proposed four types of IGP: (1) opportunistic, when IGP is a fortuitous event, (2) nutritional, when nutritional benefits are associated with the eating of an IG prey, (3) competitive, when eating the IG prey eliminates an important competitor, and (4) protective, when eating the IG prey eliminates a potential predator under conditions of symmetrical IGP. In the first type, the IG predator does not explicitly search for IG prey, whereas in the three others it actively hunts IG prey because of the benefits of killing or eating them. Therefore, the type of IGP, and probably hunting strategy, are described by specific values of search rate (Rosenheim and Corbett 2003, Lucas 2005, Schmitz 2007). Accounting for search rate variations in functional response models would be a promising approach to investigate the effects of IGP type and predator searching behavior on IGP frequency, which may have important repercussions on overall food web dynamics.

Population dynamics models using a linear functional response predict that food webs that include IG interactions are unstable and not persistent, especially at higher productivity levels (Holt and Polis 1997, Borer et al. 2007, Holt and Huxel 2007). However, as we discussed above, linear functional responses do not impose limits on predation rate (Fig. 1A), which induce strong interactions and an overestimated predator reproductive numerical response at higher prey density. As a consequence, linear functional responses tend to be destabilizing in terms of demographic fluctuations and species coexistence (McCann et al. 1998, Abrams and Fung 2010). On the other hand, nonlinear functional response limits predation rate at higher prey density (Fig. 1B) and thus weakens the strength of interactions and the predator reproductive numerical response, which in turn dampens oscillations between consumers and resources, promoting community persistence even at higher productivity (McCann and Hastings 1997, McCann et al. 1998, Uchida et al. 2007, Abrams and Fung 2010). However, other studies pointed out that Type II functional response alone does not sufficiently decrease top-down pressure and population oscillations to explain the persistence of the IG prey in productive environment (Mylius et al. 2001, Revilla 2002, Krivan and Diehl 2005, Rall et al. 2008). Nevertheless, Abrams and Fung (2010) recently demonstrated that the influence of Type II functional response on community stability and persistence depends on the range of functional response parameters included in food web models. This finding is illustrated by the elegant field study carried out by Emmerson and Raffaelli (2004) in which they examined predator–prey interaction strengths in the Ythan Estuary food web and then parameterized food web models using their experimental parameters. They found that food web models were always dynamically stable mainly because they were able to refine parameter space using their empirical knowledge of the real ecosystem. This study, together with results from Abrams and Fung (2010), highlights the need of empirical data to parameterize theoretical models and then generate realistic predictions about interaction strength and food web dynamics. This may be particularly important given that parameter combinations representative of realistic model ecosystems probably represent only a tiny fraction of the full parameter space.

Despite numerous theoretical models on IGP and productivity, there are still very few empirical studies testing model assumptions and predictions, probably because of the complexity of IGP systems. In this study, we have tried to bridge the gap between theory and experimental results by providing the first empirical analysis of the functional response of an IG predator. We found that the Type II functional response model is a good predictor of intraguild predation and allows a good understanding of how environmental productivity and predator behavior influence the occurrence and outcome of intraguild predation. Our study also highlights the urgent need of better empirical data to parameterize theoretical models and test some of their basic assumptions. This would help to improve theoretical models and thereby our understanding of species interactions and community dynamics.

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SUPPLEMENTAL MATERIAL

APPENDIX

CALCULATION DETAILS FROM EQ. 8 TO EQ. 9

Starting with the model (Eq. 8) for *C. maculata* exploiting intra- or extraguild prey with a similar search rate ($a_{eg} = a_{ig}$):

$$N_{eg} = N_{0eg} \times \left(1 - e^{-a_{eg}(t - h_{eg}N_{eg} - h_{ig}N_{ig})}\right) \tag{A.1}$$

$$N_{ig} = N_{0ig} \times \left(1 - e^{-a_{eg}(t - h_{ig}N_{ig} - h_{eg}N_{eg})}\right). \tag{A.2}$$

We used the Lambert *W* function to solve recursive functions A.1 and A.2 (see Bolker 2008 for details). This yields:

$$N_{eg} = N_{0eg} - \frac{w\left(a_{eg}h_{eg}N_{0eg}e^{-a_{eg}(t - h_{eg}N_{0eg} - h_{ig}N_{ig})}\right)}{a_{eg}h_{eg}} \tag{A.3}$$

$$N_{ig} = N_{0ig} - \frac{w\left(a_{eg}h_{ig}N_{0ig}e^{-a_{eg}(t - h_{ig}N_{0ig} - h_{eg}N_{eg})}\right)}{a_{ig}h_{ig}}. \tag{A.4}$$

Inserting Eq. A.4 into Eq. A.3 yields:

$$N_{eg} = N_{0eg} - \frac{w(a_{eg}h_{eg}N_{0eg}e^{-a_{eg}(t - h_{eg}N_{0eg} - h_{ig}(N_{0ig} - \frac{w(a_{eg}h_{ig}N_{0ig}e^{-a_{eg}(t - h_{ig}N_{0ig} - h_{eg}N_{eg})})}{a_{ig}h_{ig}}))})}{a_{eg}h_{eg}}. \tag{A.5}$$

By reversing the Lambert *W* function:

$$-a_{eg}h_{eg}(N_{eg} - N_{0eg})e^{-a_{eg}h_{eg}(N_{eg} - N_{oeg})} = a_{eg}h_{eg}N_{0eg}e^{-a_{eg}(t - h_{eg}N_{0eg} - h_{ig}(N_{0ig} - \frac{w(a_{eg}h_{ig}N_{0ig}e^{-a_{eg}(t - h_{ig}N_{0ig} - h_{eg}N_{eg})})}{a_{ig}h_{ig}}))} \tag{A.6}$$

By simplification:

$$-(N_{eg} - N_{0eg})e^{-a_{eg}h_{eg}N_{eg}} = N_{0eg}e^{-a_{eg}(t - h_{ig}(N_{0ig} - \frac{w(a_{eg}h_{ig}N_{0ig}e^{-a_{eg}(t - h_{ig}N_{0ig} - h_{eg}N_{eg})})}{a_{ig}h_{ig}}))} \tag{A.7}$$

$$-(N_{eg} - N_{0eg})e^{-a_{eg}h_{eg}N_{eg}} = N_{0eg}e^{-a_{eg}(t - h_{ig}N_{0ig})}e^{-w(a_{eg}h_{ig}N_{0ig}e^{-a_{eg}(t - h_{ig}N_{0ig} - h_{eg}N_{eg})})}. \tag{A.8}$$

Given that

$$e^{w(x)}w(x) = x$$

and

$$e^{-w(x)} = \frac{w(x)}{x}$$

Eq. A.8 is equal to:

$$-(N_{eg} - N_{0eg})e^{-a_{eg}h_{eg}N_{eg}} = N_{0eg}e^{-a_{eg}(T - h_{ig}N_{0ig})}w(a_{eg}h_{ig}N_{0ig}e^{-a_{eg}(t - h_{ig}N_{0ig} - h_{eg}N_{eg})})\frac{e^{a_{eg}(t - h_{ig}N_{0ig} - h_{eg}N_{eg})}}{a_{eg}h_{ig}N_{0ig}}. \tag{A.9}$$

By simplification:

$$-(N_{eg} - N_{0eg})a_{eg}h_{ig}\frac{N_{0ig}}{N_{0eg}} = w(a_{eg}h_{ig}N_{0ig}e^{-a_{eg}(t - h_{ig}N_{0ig} - h_{eg}N_{eg})}). \tag{A.10}$$

Given that

$$w^{-1}(x) = xe^{x}$$

Eq. A.10 is equal to:

$$-(N_{eg} - N_{0eg})a_{eg}h_{ig}\frac{N_{0ig}}{N_{0eg}}e^{-(N_{eg} - N_{0eg})a_{eg}h_{ig}\frac{N_{0ig}}{N_{0eg}}} = a_{eg}h_{ig}N_{0ig}e^{-a_{eg}(t - h_{ig}N_{0ig} - h_{eg}N_{eg})}. \tag{A.11}$$

By simplification:

$$-\frac{(N_{eg}-N_{0eg})}{N_{0eg}}e^{-N_{eg}a_{eg}h_{ig}\frac{N_{0ig}}{N_{0eg}}}=e^{-a_{eg}(t-h_{eg}N_{eg})} \tag{A.12}$$

then:

$$-\frac{(N_{eg}-N_{0eg})}{N_{0eg}}e^{-N_{eg}a_{eg}h_{ig}\frac{N_{0ig}}{N_{0eg}}+h_{eg}}=e^{-a_{eg}t} \tag{A.13}$$

then:

$$-a_{eg}\left(h_{ig}\frac{N_{0ig}}{N_{0eg}}+h_{eg}\right)(N_{eg}-N_{0eg})e^{-(N_{eg}-N_{0eg})a_{eg}\left(h_{ig}\frac{N_{0ig}}{N_{0eg}}+h_{eg}\right)}=a_{eg}\left(h_{ig}\frac{N_{0ig}}{N_{0eg}}+h_{eg}\right)N_{0eg}e^{-a_{eg}t+N_{0eg}a_{eg}\left(h_{ig}\frac{N_{0ig}}{N_{0eg}}+h_{eg}\right)}. \tag{A.14}$$

Applying w to each side yields:

$$-a_{eg}\left(h_{ig}\frac{N_{0ig}}{N_{0eg}}+h_{eg}\right)(N_{eg}-N_{0eg})=w\left(a_{eg}\left(h_{ig}\frac{N_{0ig}}{N_{0eg}}+h_{eg}\right)N_{0eg}e^{-a_{eg}t+N_{0eg}a_{eg}\left(h_{ig}\frac{N_{0ig}}{N_{0eg}}+h_{eg}\right)}\right) \tag{A.15}$$

then:

$$N_{eg}=N_{0eg}\left(1-\frac{w\left(a_{eg}(h_{ig}N_{0ig}+h_{eg}N_{0eg})e^{-a_{eg}(t-h_{ig}N_{0ig}-h_{eg}N_{0eg})}\right)}{a_{eg}(h_{ig}N_{0ig}+h_{eg}N_{0eg})}\right) \tag{A.16}$$

and:

$$N_{eg}+N_{ig}=(N_{0eg}+N_{0ig})\times\left(1-\frac{w\left(a_{eg}(h_{eg}N_{0eg}+h_{ig}N_{0ig})\times e^{-a_{eg}(t-h_{eg}N_{0eg}-h_{ig}N_{0ig})}\right)}{a_{eg}(h_{ig}N_{0ig}+h_{eg}N_{0eg})}\right). \tag{A.17}$$