INTRAGUILD PREDATION AMONG APHID PREDATORS: CHARACTERIZATION AND INFLUENCE OF EXTRAGUILD PREY DENSITY

ÉRIC LUCAS,[1] DANIEL CODERRE,[2] AND JACQUES BRODEUR[1]

[1]*Centre de recherche en horticulture, Département de phytologie Université Laval, Sainte-Foy, Québec, Canada G1K 7P4*
[2]*Département des Sciences Biologiques, Université du Québec à Montréal, C.P. 8888 Succursale "Centre Ville,"
Montréal, Québec, Canada H3C 3P8*

Abstract. Intraguild predation (IGP), a common interaction in invertebrates and vertebrates, affects the abundance and distribution of many species. Several parameters influence the magnitude and direction of IGP: feeding specificity, size, mobility, and aggressiveness of the protagonists, as well as extraguild prey density. Under laboratory conditions, we studied IGP among three species of aphid predators, *Aphidoletes aphidimyza* (Diptera: Cecidomyiidae), *Chrysoperla rufilabris* (Neuroptera: Chrysopidae), and *Coleomegilla maculata lengi* (Coleoptera: Coccinellidae), which commonly attack the potato aphid (extraguild prey) *Macrosiphum euphorbiae* (Homoptera: Aphididae). We characterized the levels and symmetry of IGP among the various stages of the predators in the absence of extraguild prey. The aphid specialist *A. aphidimyza* was more vulnerable to IGP than *C. rufilabris* and *C. maculata,* two generalist predators. The *C. maculata*/*C. rufilabris* interaction was symmetric (mutual IGP), whereas the *C. maculata*/*A. aphidimyza* and *C. rufilabris*/*A. aphidimyza* interactions were asymmetric, in favor of the coccinellid and the lacewing, respectively. Sessile and low mobility stages of all species were extremely vulnerable to IGP. Generally, the larger sized individual won confrontations. For similar sizes, lacewing larvae were superior to coccinellid larvae.

We also tested whether IGP decreases when extraguild prey are introduced into the system. Data from five predator combinations revealed three types of responses: (1) an exponential decrease in IGP (lacewing instar I vs. coccinellid instar I); (2) a constant IGP (lacewing instar III vs. coccinellid instar I); (3) a constant IGP at low densities decreasing at high densities (lacewing instar III vs. gall midge old larva). Four theoretical scenarios are derived from these responses. Each is discussed according to the ecological attributes of the protagonists. This study shows that IGP is influenced by factors inherent to the predators and external factors such as extraguild prey density. The results are discussed further in the context of aphid biological control.

Key words: aphid predator; Aphidoletes aphidimyza; *biological control;* Chrysoperla rufilabris; Coleomegilla maculata; *feeding specificity; intraguild predation;* Macrosiphum euphorbiae; *predator–prey interaction; prey density; prey size.*

INTRODUCTION

Intraguild predation (IGP) occurs when one species in a predatory guild feeds on another predatory species within the guild. The aggressor is the intraguild predator (IG predator), the victim the intraguild prey (IG prey), and the common resource is the extraguild prey. As outlined by Polis et al. (1989), IGP is considered to be an extreme form of competition or a type of classical predation that may affect the distribution, abundance, and evolution of animal species. IGP not only provides an additional food resource to IG predators, it may reduce inter- or intraspecific competition and predation risk in the cases of mutual IGP. IGP may represent an important mortality factor that can produce local extinctions of IG prey populations; conversely, it can increase IG prey abundance by causing a compensatory decrease in intraspecific competition. At the

community level, IGP can cause spatial and temporal segregation of intraguild predators and prey, with the IG prey restricted to less suitable habitats or periods (Sih et al. 1985, Hurd and Eisenberg 1990, Moran et al. 1996).

Size and the degree of feeding specificity of the protagonists are two important factors that determine the nature, symmetry, and outcome of IGP. IGP occurs mainly with generalist predators that attack prey of smaller size, including conspecifics (Polis 1981, Polis et al. 1989). In most taxa, the incidence of mortality is inversely correlated with size, with smaller individuals being more vulnerable and threatened by more predators (Werner and Gilliam 1984). This, however, is not always the case as small individuals can eat larger individuals (Polis et al. 1989, Fincke 1992). Furthermore, the hierarchy of IGP may change because of predator ontogeny (Hurd 1988, Wissinger 1989). Implicitly, a specialist predator should be less adapted to attacking a nonpreferred prey, and thus be at a disad-

vantage during confrontations with generalist predators. The mobility of protagonists also determines the outcome of IGP, fleeing being one of the most common and effective defensive strategies of prey (Edmunds 1974, Sih 1987). Sessile stages, or those with reduced mobility, are particularly vulnerable since they are more easily captured (New 1991).

Although it is clear that extraguild prey can influence the nature and issue of IGP (Polis et al. 1989), the link between extraguild prey density and level of IGP in terrestrial and aquatic communities has not been fully explored. Specifically, a few experimental studies showed a gradual reduction in IGP levels with increased extraguild prey density; this indicates that when a predator's usual prey are rare or unavailable, the predator may broaden its diet to include new organisms such as other predator species in the same guild (Bailey and Polis 1987). More studies have investigated the effects of food (extraguild prey) on cannibalism (Fox 1975, Polis 1981), and different patterns of extraguild prey and predator density dependence have been described (see Dong and Polis 1992). In most cases, cannibalism increases as the abundance of extraguild prey or alternative food decreases.

We use a system, the potato aphid *Macrosiphum euphorbiae* (Thomas) (Homoptera: Aphididae) and three aphidophagous predators (the lacewing *Chrysoperla rufilabris* Burmeister, the spotted lady beetle *Coleomegilla maculata lengi* Timberlake and the gall midge *Aphidoletes aphidimyza* Rondani), which has several advantages to study IGP. *Coleomegilla maculata* and *C. rufilabris* are generalist predators that actively search for prey (Canard and Duelli 1984). Both adult and larval stages of *C. maculata* are predaceous, whereas only *C. rufilabris* larvae are predators. *Aphidoletes aphidimyza* is a furtive predator specialized on aphids (New 1991). Larvae creep and paralyze aphids before extracting the body contents. Aphid/predator interactions, as well as the predators' searching strategies, are well known for *C. maculata* (Frazer 1988a), *C. rufilabris* (Canard and Duelli 1984), and *A. aphidimyza* (Markkula and Tiittanen 1985, Nijveldt 1988). The three predatory species have overlapping niches and may coexist in the field (Boiteau 1983, Frazer 1988b). They are commercially available and can be used in conjunction to suppress aphids in biological control programs. Furthermore, rearing of parthenogenetic aphids easily generates a great number of identical extraguild prey for tests.

Our first objective was to characterize, under laboratory conditions, the occurrence of IGP between all stages of each predatory species in the absence of extraguild prey. We predicted that (1) the specialist *A. aphidimyza* will be a victim of IGP following confrontations with the generalist predators *C. maculata* and *C. rufilabris*; (2) sessile or slow-moving stages will be victims of IGP by mobile stages; (3) larger sized protagonists will win the confrontations. The second objective was to test the hypothesis that IGP decreases when the extraguild prey density increases.

METHODS

A colony of potato aphids, *M. euphorbiae,* established from individuals collected near Québec City (Canada), was maintained on potato plants, cv. Norland. *Chrysoperla rufilabris* and *C. maculata* were purchased from Groupe Biocontrôle Inc. (Sainte-Foy, Canada) and *A. aphidimyza* from Plant Products Inc. (Montréal, Canada). Upon receipt, they were reared in the laboratory on *M. euphorbiae.* All colonies were maintained at $20° \pm 1°C$, 60–70% relative humidity, and under a photoperiod of 16L:8D.

IGP in the absence of aphids (extraguild prey)

We first characterized, in the absence of prey, the level and symmetry of IGP among the different stages of each of the three predator species. Combinations of two predators were chosen based on predator (1) developmental stage (eggs, larvae, pupae, and adults), (2) size (eggs and young larvae vs. old larvae and adults), and (3) mobility [sessile (eggs, pupae), slightly mobile (gall midge larvae), and highly mobile individuals (coccinellid and lacewing larvae, adults)]. Obviously, combinations of nonpredatory stages were not included. The 37 tested combinations are shown in Figs. 1, 2, and 3.

Predators of a specific age class were obtained by rearing neonate larvae in synchronous cohorts until they reached the desired stage. Coccinellid and lacewing larvae were used in the test 48 h after molting. Gall midges were classified as "young" (<48 h) and "old" larvae (>168 h) since there is a controversy over the number of *A. aphidimyza* larval stages (Markkula and Tiittanen 1985). Predators were starved for 24 h prior to testing in order to increase their motivation to forage. Tests were carried out in growth chambers at $25° \pm 1°C$, 70% relative humidity, and 16L:8D.

Two experimental setups maximizing interactions between predators were used. The first one, for *C. maculata*/*C. rufilabris* interactions, used a plastic funnel (7.5 cm in height $\times$ 9.8 cm in diameter) coated with fluon to prevent the insects from escaping, a lid with a meshed opening (muslin) and a jar (12.5 $\times$ 6 cm) filled with water into which the funnel was introduced. A potato plant stem bearing a single mature leaf was placed in the funnel. The basal section of the stem was plunged into the water and fixed with modeling clay onto the funnel's bottleneck. For treatments involving *A. aphidimyza,* a second setup, consisting of a petri dish (5 cm in diameter) covered with a moistened filter paper, was used as preliminary tests showed that young larvae were often found dying on the funnel surfaces.

In all combinations involving eggs, they were placed in groups of five in a manner analogous to their natural distribution: in a mass for *C. maculata,* in a loose mass for *A. aphidimyza,* and scattered for *C. rufilabris.* Lace-
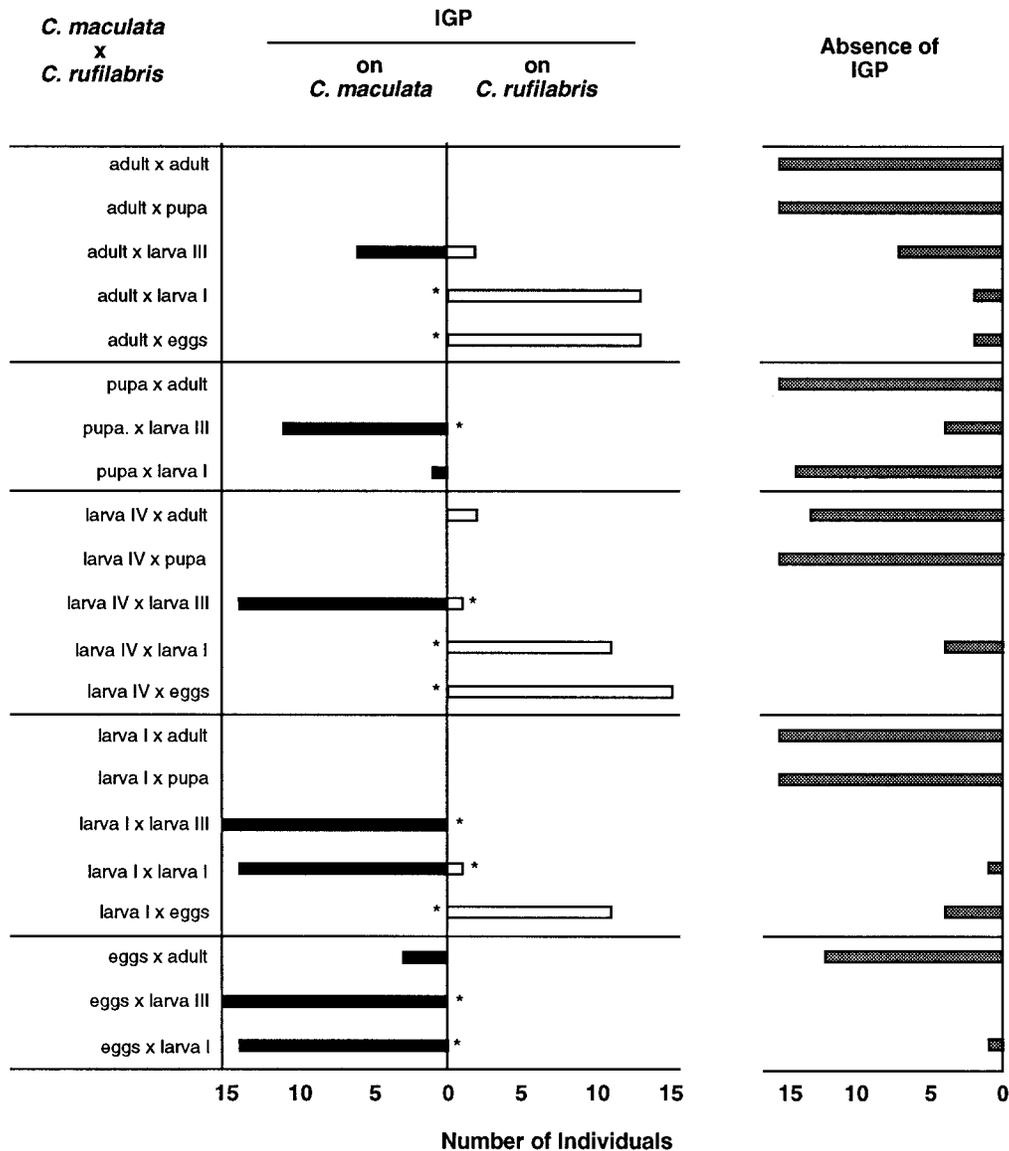
FIG. 1. Intraguild predation (IGP) between various developmental stages of *Coleomegilla maculata* and *Chrysoperla rufilabris* in the absence of aphids. The solid and open bars represent the numbers of *C. maculata* and *C. rufilabris* killed. The shaded bars (right) show the number of interactions where no IGP was recorded. Asterisks indicate significant asymmetry for that combination of predators (χ^2, df = 2, $P < 0.05$).

wing eggs were glued at their stalk (Lepage bondfast) on the upper leaf surface, in their natural position. Coccinellid eggs were placed along the midvein of the upper leaf surface, and those of *A. aphidimyza* in the center of the filter paper. Pupae were glued near the midvein of the lower leaf surface. Larvae and adults were introduced on the upper surface of the leaf at opposite ends. Tests were conducted with one individual of each of the two predator species, except for eggs.

After 24 h, predators were recovered, examined under a stereo microscope, and survival determined. Evidence of consumption of the IG prey was used to distinguish IGP from natural mortality. Control treatments

and data from IGP experiments showed that natural mortality was low (from 0 to 6.7%), except for adults of *A. aphidimiza* and pupae of *C. maculata* where 11.7 and 16.7% of the control individuals died within 24 h, respectively. IGP on eggs was scored when at least one egg from the mass was consumed. IGP on coccinellid pupae was estimated from the percentage of adult emergence adjusted for natural mortality, as punctures made on pupae by chrysopids were not obvious. In this instance, 20 pupae were maintained under experimental conditions to determine the proportion of emergence in the absence of IGP. A level of IGP (IL; proportion of replicates with IGP over the total number of repli-
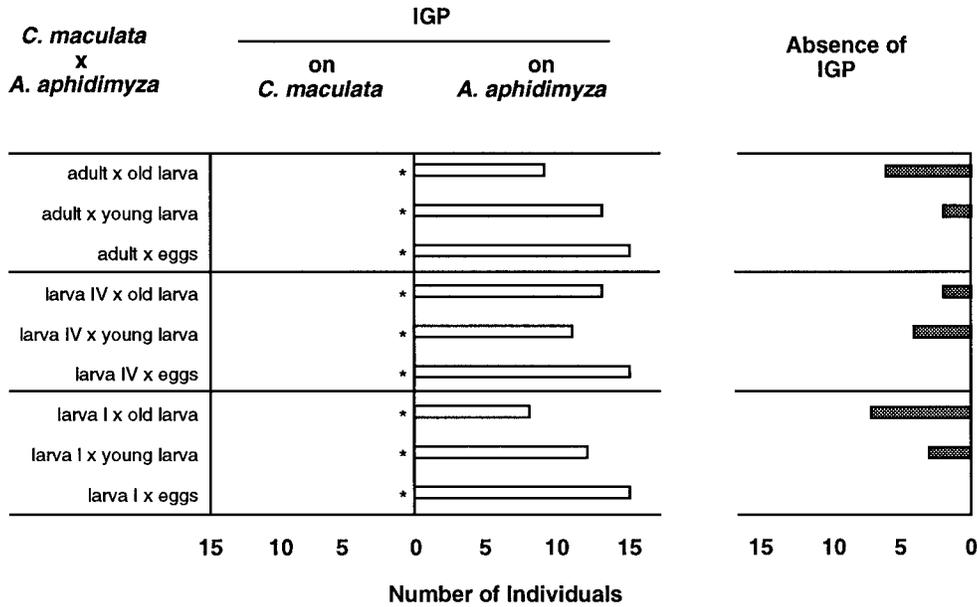
FIG. 2. Intraguild predation (IGP) between *Coleomegilla maculata* and *Aphidoletes aphidimyza* in the absence of aphids. The open bars represent the number of *A. aphidimyza* killed. The shaded bars (right) show the number of interactions where no IGP was recorded. Asterisks indicate significant asymmetry for that combination of predators (χ^2, df = 2, $P < 0.05$).

cates) as well as an index of symmetry (SI; proportion of replicates in which a given predator was eaten over the total number of replicates in which there was IGP) were calculated for each pair of predators. Fifteen replicates per combination of predators were carried out.

The indices of symmetry for each tested pair were compared to a theoretical index of 50% corresponding to a symmetric interaction using a test of conformity (Scherrer 1984). Following arcsine transformation, the

mean number of eggs consumed per treatment were analysed using a one-way ANOVA.

IGP in the presence of aphids (extraguild prey)

In order to determine the effect of extraguild prey on IGP, we first compared IGP levels in the absence or presence of aphids. From the results of the previous experiment, five predator combinations were chosen based on the level of IGP (IL), the index of symmetry
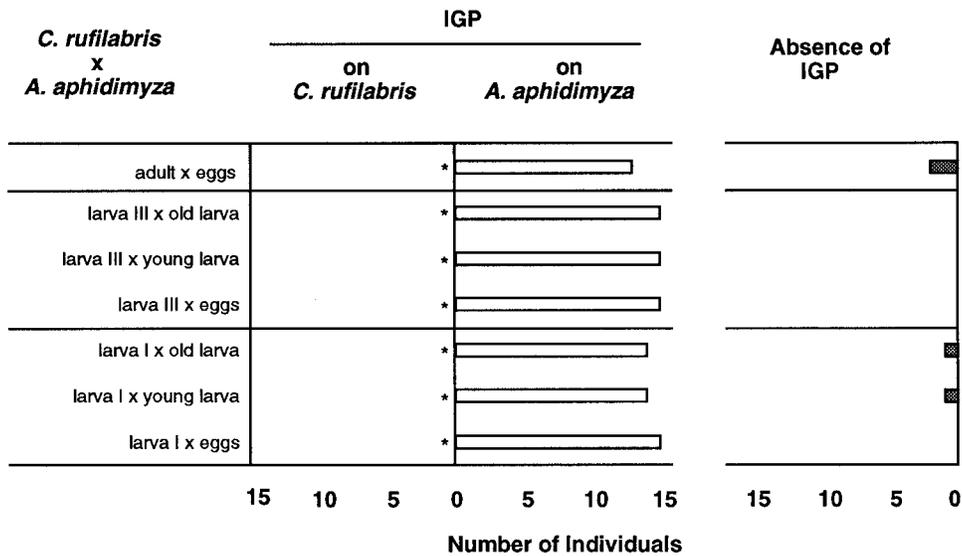

FIG. 3. Intraguild predation (IGP) between *Chrysoperla rufilabris* and *Aphidoletes aphidimyza* in the absence of aphids. The open bars represent the number of *A. aphidimyza* killed. The shaded bars (right) show the number of interactions where no IGP was recorded. Asterisks indicate significant asymmetry for that combination of predators (χ^2, df = 2, $P < 0.05$).

TABLE 1. Level of IGP (intraguild predation) and symmetry of IGP among five predator combinations without extraguild (aphid) prey. These combinations were used in the experiment to assess the effect of extraguild prey density on IGP.

	Species/stage		Mobility† (Pred. 1/ Pred. 2)	IL‡ (%)	SI§ (%)
Combination	Predator 1	Predator 2			
1	*C. maculata*/LI	*C. rufilabris*/LI	++/++	93	7
2	*C. maculata*/LI	*C. rufilabris*/LIII	++/+++	100	0
3	*C. maculata*/LI	*A. aphidimyza*/OL	++/+	53	100
4	*C. rufilabris*/LI	*A. aphidimyza*/eggs	++/0	100	100
5	*C. rufilabris*/LIII	*A. aphidimyza*/OL	+++/+	100	100

† Mobility ranked as: +++ high, ++ moderate, + low. 0 indicates sessile stage.
‡ IL = level of IGP.
§ SI = index of symmetry (100% indicates unidirectional interaction, i.e., the first predator always kills the second one).

(SI), and the mobility of predators so as to obtain an array of possibilities (Table 1).

A population of early second-instar aphids was introduced in the experimental setup on plant material 24 h prior to testing. The aphid density was fixed at twice the number consumed by the two predators in a 24-h period, as determined by preliminary experiments. Predators were introduced within the system as described above and the occurrence of IGP determined after 24 h. Fifteen replicates were used for each treatment.

Levels of IGP in the absence (control) or in the presence of aphids were compared using a chi-square test (Scherrer 1984). Following arcsine transformation, the mean number of eggs consumed in the presence and absence of prey was compared using an ANOVA.

The effect of extraguild prey on IGP was further studied for three combinations of predators at seven different densities of aphids. Based on the results from the previous experiment on the effect of aphids on IGP, we selected three combinations that showed (1) the greatest reduction in IGP (93 to 0%, *C. rufilabris* LI × *C. maculata* LI), (2) a constant level of IGP in the presence of prey (100 to 100%, *C. rufilabris* LIII × *C. maculata* LI), and (3) a nonsignificant intermediary decrease in IGP (100 to 87%, *C. rufilabris* LIII × *A. aphidimyza* late larva). Each one was tested with the following prey densities: 0, 0.25, 0.5, 1, 1.5, 2, and 3×. The corresponding numbers of aphids are shown in Fig. 5. Tests with third instar lacewings were conducted on plants bearing two leaves because of the high aphid densities required. Predators were introduced at the leaf extremities and experimental conditions were the same as described above.

Differences in IGP levels were tested using contingency tables. The general test was followed by a multiple comparisons test corresponding to the experimentwise error rate (Scherrer 1984), which consists in recalculating the alpha significance level (original α = 0.05) and comparing the groups two by two using a *G* test.

RESULTS

IGP in the absence of aphids (extraguild prey)

C. maculata × *C. rufilabris.*—There was no IGP in 49% of the tests between the coccinellid and the lacewing. However, when IGP occurred all developmental stages of both predators were involved, except for lacewing pupae (Fig. 1). Coccinellid egg masses were highly vulnerable to lacewing larvae and, to a lesser extent, to adults. Third-instar larvae consumed 97% of the eggs from a mass, more so than to early larval instars (61%) and adults (4%) (ANOVA, $F = 55.6$, df = 2, 42, $P < 0.0001$). Similarly, lacewing egg masses were frequently attacked by coccinellids. A large proportion of eggs within a mass were eaten by coccinellid fourth larval instars (84%) and adults (75%), whereas early instars consumed significantly fewer eggs (24%) (ANOVA, $F = 14.7$, df = 2, 42, $P = 0.0001$).

Young larvae were attacked by old larvae and, in the case of lacewings, by adult coccinellids. Notably, for an equivalent predator size, lacewing larvae won confrontations with coccinellid larvae. Lacewing LIII frequently fed on coccinellid pupae, whereas lacewing pupae were not attacked by coccinellids. Only a few adult lacewings were killed by *C. maculata* LIV.

Results indicate significant asymmetrical interactions between protagonists, except for the adult coccinellid × lacewing LIII interaction. However, at the species level, IGP could be considered mutual between *C. maculata* and *C. rufilabris*.

C. maculata × *A. aphidimyza.*—IGP occurred in nearly 72% of the tests involving the coccinellid and the gall midge. The interaction was always asymmetric and favoring the coccinellid (Fig. 2). All tested *A. aphidimyza* stages were vulnerable to coccinellid adults and larvae.

C. rufilabris × *A. aphidimyza.*—Ninety-six percent of the tests involving the lacewing and the gall midge resulted in IGP. As with *C. maculata,* IGP was highly asymmetric favoring the lacewing (Fig. 3).

The proportion of *A. aphidimyza* eggs from a mass attacked by lacewings and coccinellids was always high (>80%), except for lacewing adults (49%) (ANOVA, $F = 11.7$, df = 5, 84, $P < 0.0001$, followed by LSD [least significant difference]).

IGP in the presence of aphids (extraguild prey)

Adding aphids modified IGP levels in several ways (Fig. 4). A significant decrease in IGP was observed
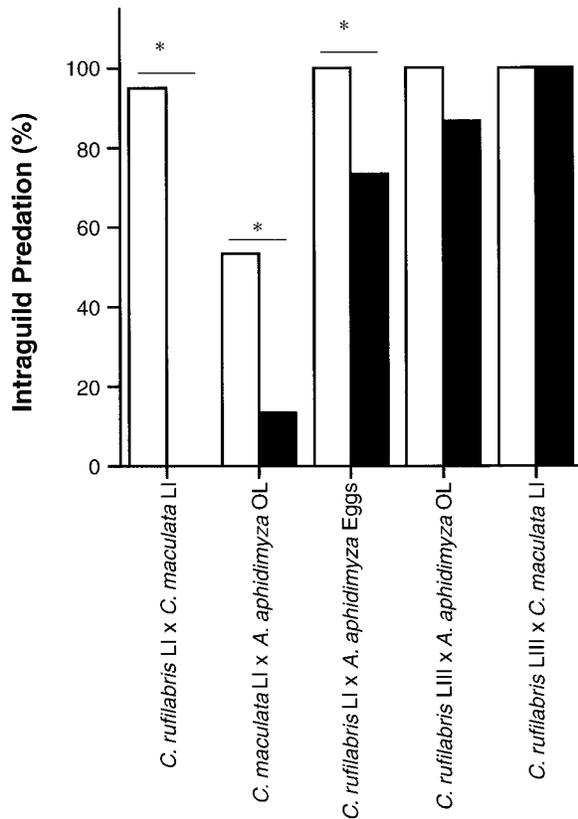
FIG. 4. Effect of aphids on the level of intraguild predation. Bars represent the percentage of replicates where one predator was killed in the absence of aphids (open bars), and with a density of aphids fixed at twice the number consumed by the two predators in a 24-h period (solid bars). Percentages followed by an asterisk are significantly different (χ^2, df = 1, $P < 0.05$). OL = old larva.

for the following pairs: coccinellid LI vs. gall midge OL ($\chi^2 = 5.4$, df = 1, $P = 0.0201$), lacewing LI vs. gall midge eggs ($\chi^2 = 12.9$, df = 1, $P = 0.0003$), and lacewing LI vs. coccinellid LI ($\chi^2 = 36.2$, df = 1, $P < 0.0001$). In the latter case, IGP completely disappeared. However, the addition of prey did not decrease IGP between lacewing LIII vs. gall midge OL ($\chi^2 = 2.1$, df = 1, $P = 0.1432$) and lacewing LIII vs. coccinellid LI.

Similarly, the mean number of gall midge eggs consumed by lacewing first-instar larvae significantly decreased from 4.8 out of 5 eggs (96%) in the absence of aphids to 1.6 out of 5 eggs (32%) in the presence of aphids (ANOVA, $F = 54.9$, df = 1, 28, $P < 0.0001$).

The effect of prey density on the level of IGP varied depending on the combination of predators tested. For the pair coccinellid LI vs. lacewing LI, which showed the largest reduction in IGP when 2× prey had been introduced in the system, the interaction was unidirectional (lacewing eating coccinellid) and IGP level decreased rapidly with increasing prey density ($\chi^2 = 77.3$, df = 6, $P < 0.0001$; Fig. 5A), whereas it remained
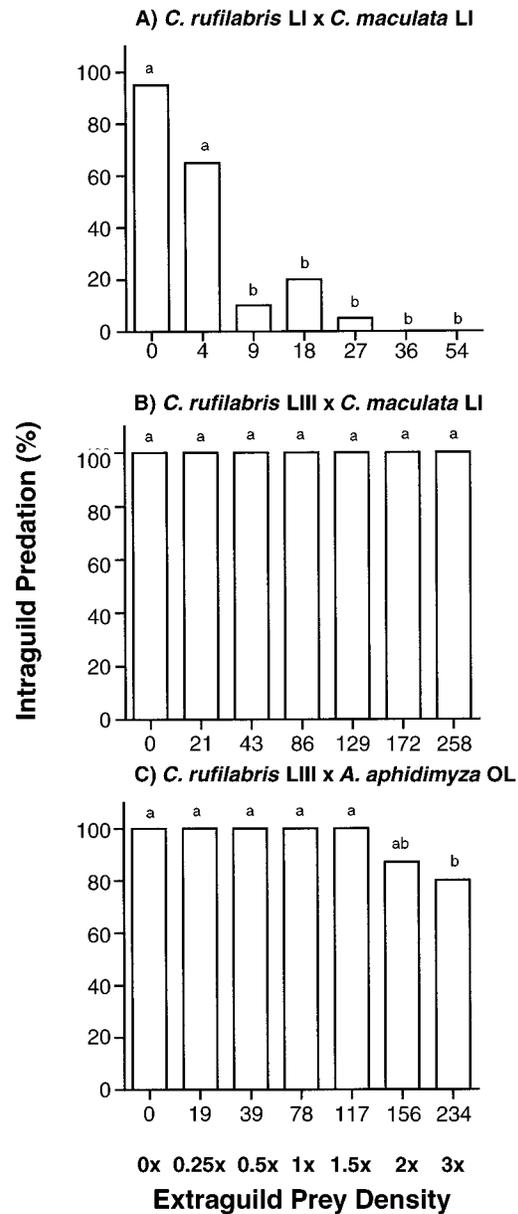

FIG. 5. Intraguild predation (IGP) as a function of aphid density. Open bars represent the percentage of replicates where one predator was killed. Percentages followed by different letters are significantly different (χ^2, df = 6, $P < 0.05$). Numbers of aphids per treatment are indicated below the *x*-axis. 1× = twice the daily consumption of both predators.

constant and maximum (100%) for the lacewing LIII vs. coccinellid LI pair ($P = 1$; Fig. 5B). For the lacewing LIII vs. gall midge OL pair, which previously showed a slight decrease in IPG with 2× prey, the level of IGP was maximum for densities 0 to 1.5×, after which it decreased, respectively, to 87 and 80% for densities 2 and 3× respectively ($\chi^2 = 8.4$, df = 2, $P = 0.015$; Fig. 5C). A significant decrease in the level of IGP was observed between initial densities and density 3× (G test, $G = 5.8$, df = 1, $P = 0.0178$).

Discussion

We characterized, under controlled conditions, the level and symmetry of IGP among three aphidophagous predatory species. In most cases, the results are consistent with our initial predictions. In the absence of extraguild prey, IGP occurred in the majority of the tested combinations, most often at very high levels. Interactions between individuals of the same developmental stage were highly asymmetric. At the species level, the relationship *C. rufilabris* × *C. maculata* was mutual IGP (Polis et al. 1989), whereas the interactions involving *A. aphidimyza* were highly asymmetric, with the gall midge always being the IG prey. Significant and nonexclusive factors influencing an organism's vulnerability to IGP, and thereby the symmetry of the interaction, were size, mobility, feeding specificity, and extraguild prey density.

In most cases, predator size ratio determined the outcome of an interaction, smaller individuals being killed by larger ones. The early developmental stages, which are the smallest sized individuals, were particularly vulnerable to predation. Nevertheless, larger size does not constitute an absolute advantage and a few exceptions occurred. Third-instar lacewing larvae attacked adult coccinellids with some success and were almost always victorious during confrontations with the larger fourth-instar *C. maculata* larvae (see also Sengonca and Frings 1985). The lacewing's advantage could be attributed either to its greater aggressiveness, or to the shape of its mouth parts, which allowed a solid hold following an attack.

With regard to the symmetry of the relationship, size, although significant, was less important than mobility of the protagonists. Confirming our prediction, sessile and slow-moving stages were heavily attacked by a mobile predator. Our results may, to a certain extent, depend upon the experimental setup we used, as it may have interfered with the escape behavior of vulnerable mobile stages. Nevertheless, ovipositing females and premolting larvae are expected to select egg-laying and pupation sites that reduce mortality by natural enemies, the avoidance of hazardous sites being one of the most widespread and efficient defensive mechanisms of sessile stages (Sih 1987).

The feeding specificity of the protagonists also influenced the outcome of the interactions. Interspecific interactions involving *A. aphidimyza* were asymmetric, both with the coccinellid and the lacewing, and IGP levels were consistently high (>82%). Larvae of the gall midge, a specialist predator of aphids, possess highly specialized mouth parts and inject a paralyzing toxin (Laurema et al. 1986). Such high specialization renders the gall midge completely ineffective toward organisms such as coccinellids and lacewings. In contrast, *C. rufilabris* (Nordlund et al. 1991) and *C. maculata* (Giroux et al. 1995) attack a large range of prey. Although we cannot discriminate between mobility and

feeding specificity in *A. aphidimyza,* and since our study involves only three species of aphid predators, our results suggest that specialist predators are more likely to become IG prey when involved in IGP interactions.

Our findings partially confirm that IGP decreases if extraguild prey are present. The significant reductions in IGP we observed following the addition of aphids occurred when the level of IGP, in the absence of prey, was either high or low. However, with some combinations of predators, the level of IGP remains stable or decreases only at very high extraguild prey densities. Increases in extraguild prey densities never modified the symmetry of the relationship between the two predators. Sengonca and Frings (1985) observed, in petri dishes, a great reduction in IGP between larvae of *C. carnea* and *Coccinella septempunctata* when aphids were added. They also found high levels of IGP on eggs and early larval stages even in the presence of aphids.

Based on the different responses we obtained, we suggest four theoretical scenarios to characterize the relationship between extraguild prey density and IGP in terrestrial invertebrates. In the first, IGP decreases steadily with increased extraguild prey density. This scenario occurs for two predators that forage for prey randomly, without their searching behavior influencing chances of meeting. For example, predation of the phytoseiid mite *Amblyseius cucumeris* by the predatory bug *Orius tristicolor* decreases with increasing densities of their common extraguild prey *Frankliniella occidentalis* (Thysanoptera) (Gillespie and Quiring 1992). Similarly, Polis and McCormick (1987) showed that the percentage of IG prey in the diet of *Pauroctonus mesaensis* (Scorpionida) increases with decreased availability of extraguild prey.

In the second scenario, IGP decreases exponentially as extraguild prey are introduced. In this instance, a confrontation presents a risk for both protagonists and, in the presence of extraguild prey, predators should avoid IGP interactions. This scenario corresponds to the situation observed with the lacewing LI and coccinellid LI pair where the index of symmetry (7%) indicates a risk of mortality for either predator. Spence and Cárcamo (1991) also observed that the addition of food in the habitat dramatically reduced IGP and cannibalism among pondskaters (Gerridae).

In the third scenario, IGP remains constant regardless of extraguild prey density. Three nonexclusive explanations may contribute to this type of response. First, IG predators face no risk in encountering and attacking IG prey. This scenario was observed between lacewing LIII and coccinellid LI. Second, aspects of predator foraging behavior (e.g., period of activity, searching pattern) increase encounter rate, a significant component of prey vulnerability (Sih and Moore 1990). Lacewings and coccinellids are active foragers and explore the plant similarly: both forage primarily along

leaf edges (Frazer 1988*b*). Third, concentration of the resources (prey) increases the risk of predator confrontation. For three species of Odonata that developed in flooded tree cavities, the smallest cavities did not allow cohabitation of two species (Fincke 1994).

In the last scenario, IGP remains constant and high at low extraguild prey densities but decreases at very high densities. Such a scenario was observed between lacewing LIII and gall midge OL. As previously described, high rates of IGP at low aphid densities occur if one predator (lacewing) runs no risk in confronting the second (gall midge). The decrease at high prey densities could be explained in two ways. First, predators benefit from selective predation on IG prey by excluding potential competitors from the habitat when extraguild prey densities are low (Spence 1983, Polis and McCormick 1987). Cannibalism in the giant damselfly *Megaloprenus coerulatus* is density dependent and functions to reduce competition for food (Fincke 1994). Second, The IG prey (gall midge) lives among the prey (aphids) and profits from a dilution effect, which increases its chances of survival (Turchin and Kareiva 1989). This midge is a furtive predator (Klingauf 1967) that triggers litttle defensive reaction by aphid prey and causes little disturbance in gregarious prey. Such furtive hunting could reduce detection of gall midges by IG predators. Similarly, larvae of the damselfly *Coenagrion hastulatum,* which possess a ''sit and wait'' strategy were less prone to IGP by dragonfly larvae than another larval dragonfly, *Leucorrhinia dubia,* which actively searches prey (Johansson 1993).

Our results have several implications for aphid biological control. As IGP represents a major ecological force within aphidophagous guilds (Rosenheim et al. 1993), and since predator mobility, size, and specificity largely determine the prevalence and symmetry of IGP, the choice and number of species to use, as well as the choice of the developmental stages to introduce, are crucial to the success of a control program. For example, introduction of sessile stages or young larval stages of coccinellids, lacewings, and gall midges should be avoided as they are susceptible to IGP. Furthermore, third-instar lacewings should not be introduced jointly with other predators as they attack the latter even at very high aphid densities. In addition to the biological attributes of the predators, the complexity of the ecosystem may influence IGP. Rosenheim et al. (1993) showed that survival of *C. carnea,* a control agent against the cotton aphid *Aphis gossypii,* decreased by 90% following IGP interactions with indigenous predators.

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