IMPACT OF INTRASPECIFIC AND INTRAGUILD PREDATION ON PREDATOR INVASION AND COEXISTENCE: CAN EXOTIC LADYBEETLES DISPLACE NATIVE SPECIES?

Paul C. J. VAN RIJN [1], Giovanni BURGIO [2], and Matt B. THOMAS [3]

[1]Netherlands Institute of Ecology (NIOO-KNAW)
Boterhoeksestraat 48
6666 GA Heteren, NL
p.vanrijn@nioo.knaw.nl

[2]DiSTA (Entomologia), Alma Mater Studiorum Università di Bologna
Viale G. Fanin 42
I-40127 Bologna, IT

[3]Department of Agricultural Sciences
Imperial College London (Wye Campus)
Wye, Ashford, Kent TN25 5AH, U.K.

ABSTRACT

Exotic predators are more likely to replace related native species when these species not only compete for similar prey species, but also predate on the offspring of the native predators. In several groups of arthropods, however, this intraguild predation (IGP) is not only mutual, but also co-occurs with intraspecific predation (ISP or cannibalism). These different processes may have counteracting effects on species invasion and coexistence. In this study, we derived simple rules that describe under which combinations of IGP and ISP a predator species is able to invade into a stable predator-prey system, and under which conditions an invasion will results in displacement or in coexistence. This theory is then applied to species pairs of exotic and native lady beetles, to test if differences in IGP and ISP may play a role in the establishment of introduced exotic ladybeetles species (Coleoptera: Coccinellidae) such as *Harmonia axyridis* in Europe and *Coccinella septempunctata* in North America. For an accurate estimation of the key processes we cannot rely on specific experimental data only, but take allometric relationships into account as well. For ladybeetles, IGP and ISP seem to be determined largely by size differences of the interacting larvae, thereby giving an overall advantage to the larger species. On the other hand, larger species generally have higher food requirements, which may give them a disadvantage in resource competition. The estimated levels of IGP, ISP and competitive ability of the interacting species can not fully explain the invasion by the two exotic ladybeetles species.

INTRODUCTION

In recent years the invasive nature of two ladybeetles (Coleoptera: Coccinellidae) has drawn considerable attention in the scientific literature. The originally Eurasian *Coccinella septempunctata* L. established and spread through the whole of North-America in the 70s and 80s (Alyokhin and Sewell 2004; Elliott *et al.* 1996). Later, in the mid 90s, the originally Asian *Harmonia axyridis* (Pallas) became established in various parts of North-America and more recently in some parts of Western Europe as well (Adriaens *et al.* 2003).

Simultaneous with their establishment in new habitats a population decline of native species was observed. The establishment of *C. septempunctata* in arable fields in North America was followed by a dramatic decline of several native ladybeetles (including *Adalia bipunctata* L.) in these fields (Alyokhin and Sewell 2004; Elliott *et al.* 1996; Evans 2004; Wheeler and Hoebeke 1995). *C. septempunctata* also became the dominant ladybeetle species in apple orchards, pushing *A. bipunctata* to a second position (Brown 2003; Brown and Miller 1998). The later establishment of *H. axyridis* in orchards resulted in a local decline of especially this other exotic *C. septempunctata* (Brown 2003), but this pattern is not yet apparent in arable fields (Nault and Kennedy 2003). In none of the cases the exotic species has resulted in the exclusion of native species.

Resource competition for aphid prey is a possible explanation for the decline in native species following the establishment of the exotic one (Evans 2004). However, no evidence is yet provided that the exotic species are better resource competitors than the native ones.

Intraguild predation (IGP) between the exotic and native ladybeetles is regarded as the most likely reason for the spread of the exotic species and the subsequent reduction of native or earlier-established species (Yasuda and Ohnuma 1999). Lab studies indeed show that the IGP by the exotic species on native species is generally bigger than the reverse predation (Snyder *et al.* 2004; Yasuda *et al.* 2004), and that IGP between the two exotic species is in favour of *H. axyridis* (Yasuda and Ohnuma 1999).

A complicating factor is that these predators not only feed on the juveniles of other predator species, but also on those from their own species. This cannibalism or Intraspecific Predation (ISP) may partly reduce the effect of IGP on population dominance.

In this study we therefore start with reviewing the theory on the combined impact of IGP and ISP on population dynamics. Then we show how the strength of the different inter- and intraspecific interaction may be calculated, and use these values to derive predictions on invasibility and species coexistence. In the second part we include resource competition in our theory. How will the various coccinelids differ in competitive ability, and how will this alter our conclusions. Finally, we will discuss the realism of our simplifying assumptions, indicate how spatial and temporal avoidance, resource partitioning and metapopulation dynamics may affect our conclusions.

IMPACT OF IGP AND ISP ON INVASION AND COEXISTENCE

THE MODEL

In order to derive simple rules on how IGP and ISP affect the chance that an exotic predator can invade a habitat and eventually replace native guild members, we consider pairs of predators that feed on the same prey and that are equal in their ability for resource competition, i.e. have equal functional and numerical responses. The occurrence of IGP and ISP is very stage-dependent, with the smaller juveniles falling victim by older and bigger stages, which requires a stage-structured predator-prey model. The simplest version has two stages only, with only the juvenile stage vulnerable for predation, with both stages feeding, and the adult stage reproducing. The strength of IGP and ISP (c_{xx}) is expressed as the attack rate on intraguild and intraspecific juveniles relative to that on the basic (aphid) prey (see Fig. 1).

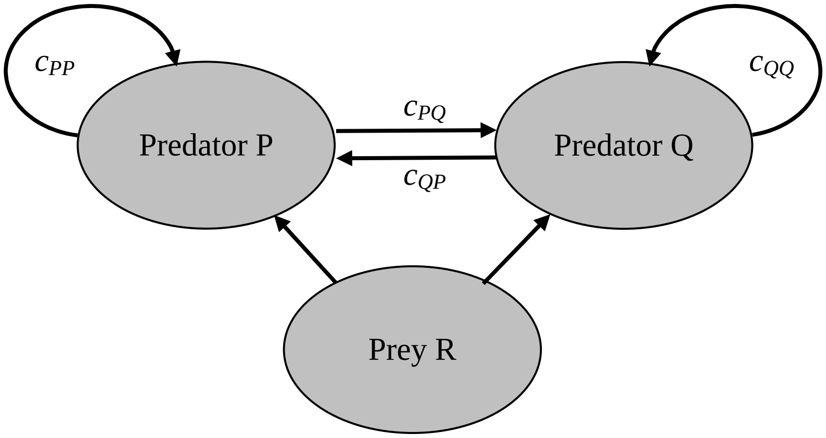

Figure 1. Food web diagram of system studied in this paper. Arrows indicate flow of biomass. Symbols show the parameters used to indicate the strength of intraspecific and intraguild predation (attack rate) relative to predation on the basic prey (resource) *R*.

In the presence of basic prey the feeding on other predators is reduced, and the reverse, according a two-prey version of Holling's disk equation (Hassell 1978). The conversion of intraguild and cannibalistic prey into predator offspring is important as well, and expressed relative to that of the basic (aphid) prey (ϕ_x).

Invasibility is studied under the assumption that a system of one predator and its prey is in equilibrium, and the question is answered: can the other predator, when still at low numbers, invade this system? When predator Q can invade a system with predator P, and predator P can invade a system with predator Q, the two predators can coexist on the same prey. By this approach the parameter conditions that allow for invasion or coexistence can be derived analytically (see van Rijn and Thomas 2005), and are shown in Fig. 2. Figure 2 shows that in absence of cannibalism no coexistence is possible. At increasing levels of cannibalism, especially when performed by both species, a wider range of IGP values leads to coexistence.

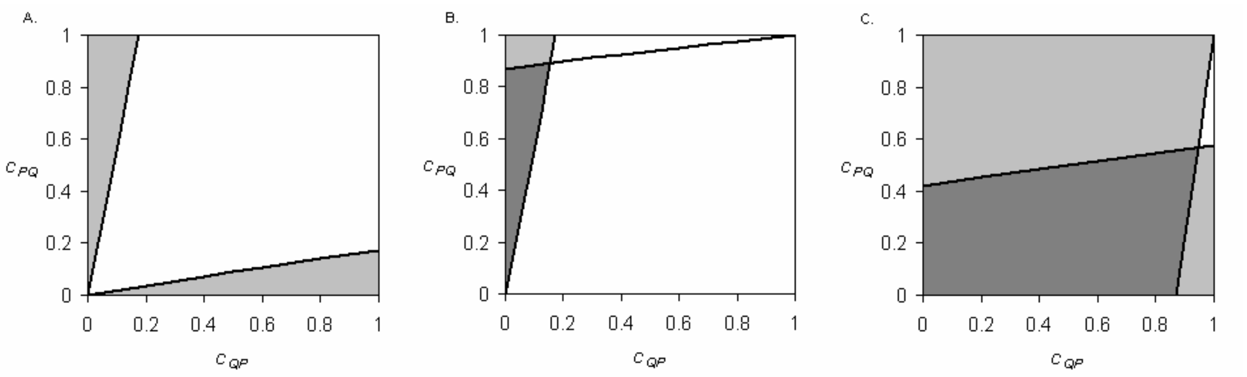

Figure 2. Mutual invasibility plots in IGP space (c_{PQ} indicates strength of IGP by species P on species Q) for different levels of ISP. A. No ISP (c_{PP}=0, c_{QQ}=0). B. ISP in P only (c_{PP}=1, c_{QQ}=0). C. ISP in both P and Q (c_{PP}=0.5, c_{QQ}=1). Light grey areas indicate IGP parameter combinations at which one species can invade the other, and dark grey areas indicate parameter combinations at which both species can mutually invade the other (allowing coexistence of P and Q).

ESTIMATING ISP AND IGP IN COCCINELLIDS

In this study we choose to focus on three species: *H. axyridis* (exotic), *C. septempunctata* (exotic in America, native in Europe), and *A. bipunctata* (native, common in America and Europe).

Experimental studies on IGP and ISP have focussed, for practical reasons, on interactions between one or two stage combinations, such as L3 - L4 (Snyder *et al.* 2004) or L2 - L2 and L2 - L4 (Yasuda *et al.* 2004). For a proper estimation of the interaction strength between the two populations all possible stage combinations should be considered. To fill this omission we utilize the commonly observed pattern that, apart for species specific effects, size difference between the two combatants strongly determine the outcome. A logistic function is fitted to the observations and used to extrapolate to unstudied interactions on the basis of the size ratio of the interaction larvae. Feeding on eggs and pupae is not considered size dependent. Conspecific eggs are strongly preferred (by all stages) over heterospecific eggs, party as a result of toxins (Agarwala and Dixon 1992). Feeding on pupae is assumed to be negligible (Schellhorn and Andow 1999). The overall intraguild or intraspecific predation rate is calculated as the mean of all the stage combinations weighed by their relative contributions to a stable population, i.e. weighed by the stage durations (including the non feeding stages, such eggs and pupae). The results of these estimations are, relative to the predation rate on aphid prey, presented in Table 1. *C. septempunctata* clearly show lower levels of cannibalism than the other species, but take intermediate positions regarding IGP (Kajita *et al.* 2000; Yasuda *et al.* 2001).

The overall conversion efficiency of cannibalistic and intraguild prey relative to aphid prey (f_x) is expected to be somewhat higher for *H. axyridis* than for the other species (Michaud and Grant 2003; Yasuda and Ohnuma 1999), but is not varied between species, and is assumed to equal 1. Other parameters (assumed to be equal for all predators) are based on the life history and predation data of *A. bipunctata* and *Myzus persicae* (Burgio *et al.* 2002; Lanzoni *et al.* 2004) and have only minor impacts on the invasion boundaries.

Table 1. Parameter (*c*) estimations for ISP and IGP for three coccinellid species and their combinations. *R** (critical resource density) estimations based on size; lower value indicates higher competitive ability.

Adult size (mm)	Predator	c-value, Victim			R* (relative to *h*)
		Ab	*Cs*	*Ha*	
4.5	*A. bipunctata*	0.32	0.25	0.19	0.26
7	*C. septempunctata*	0.35	0.22	0.25	0.39
8	*H. axyridis*	0.39	0.35	0.51	0.45

PREDICTIONS

The preceding theory and the given parameter estimations predict different outcomes for each of the three combinations of coccinellid predators, as shown in Fig. 3. *C. septempunctata* is able to invade a system with the native *A. bipunctata*. But since *A. bipunctata* is not able to invade a system with *C. septempunctata*, *C. septempunctata* will gradually displace *A. bipunctata*. *H. axyridis* is also able to invade a system with *A. bipunctata*, but reversely as well, so that the two species can coexist. Finally, the exotic *H. axyridis* may be able to invade a system with *C. septempunctata*, but this is uncertain, as the point is close to the invasion boundery. Since *C. septempunctata* is able to invade *H. axyridis*, the interaction will not result in its full displacement.

That, according to these calculations, *H. axyridis* will not displace *A. bipunctata* whereas the less aggressive predators *C. septempunctata* will, results from the relatively high level of cannibalism in *H. axyridis*, which, as shown before, creates room for coexistence.

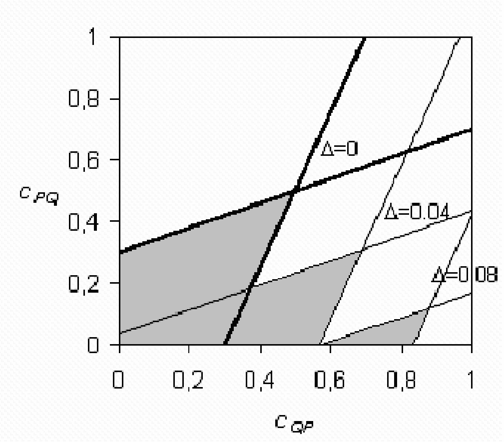

Figure 3. Mutual invasibility plot for unequal predators, based on linear functional responses. Difference in resource utilisation (*R**) between predator species is indicated by Dð, which is positive when in the advantage of *P*. IGP parameter combinations that allow for species coexistence are represented by the shaded area below and left of the two invasion bounderies. ISP levels are assumed to be moderate ($c_{PP} = c_{QQ} = 0.5$).

IMPACT OF RESOURCE COMPETITION

MODEL EXTENSIONS

Under well-mixed conditions and in absence IGP or other types of interference, the outcome of competition is predicted by Tilman's *R** rule (Tilman 1982). This rule says that the species that can maintain an equilibrium population at a lower resource (or prey) density (*R**) than other species, will outcompete these other species. Since at equilibrium reproduction equals mortality, these *R** levels result from the way reproduction and mortality is affected by prey density, i.e. the numerical response. When differences in competitive ability (differences in *R**) are incorporated in the preceding theory, the results become much more complex (see van Rijn and Thomas 2005). The basic impact, however, can be shown graphically, see Fig. 3. Increasing the competitive differences between the two predators will shift the different invasion boundaries on one direction. The positive parameter domain that allow for coexistence will consequently shrink and will ultimately become nonexistent.

ESTIMATING COMPETITIVE ABILITY IN COCCINELLIDS

Studies on the functional and numerical response of coccinellids are generally too sparse and variable to quantify differences between species. To overcome this gap in experimental data, we draw on the theory of allometric relations. The relative uniformity within the group of aphidophagous ladybeetles makes us expect that differences in prey consumption and utilisation will to a large extent result from the differences in their sizes (Dixon 2000).

Critical for the position of *R** is the shape of the functional response, and especially its half-saturation density (*h*). This parameter can be seen as prey handling rate divided by effective search rate. Since both these parameters should similarly scale with size, *h* is therefore expected to be largely independent of predator size (Gurney and Nisbet 1998). The scaling parameters of other critical parameters were estimated by analysing published data on Coccinellidae (see also Dixon 2000; Sabelis and van Rijn 1997). We estimated that maximum consumption rate and basal maintenance rate scales with length to the power 1.5 and 2.3 respectively, resulting in a scaling parameter for reproduction of 1.3.

Given the dependency of the prey equilibrium these parameters (van Rijn *et al.* 2002), *R** will increase with predator size, indicating that smaller species are better competitors. Another conclusion is that bigger species require a higher level of food supply than smaller ones to survive, which is confirmed by experiment. The study by Giles *et al.* (2002) shows that to obtain similar levels of survival *C. septempunctata* requires a higher level of food supply than the smaller *Hippodamia convergens*. The comparative studies by Obrycki *et al.* (1998) and Yasuda and Kimura (2001) show that at low prey supply the starvation related mortality of *C. septempunctata* and H. *axyridis* is much higher than of the smaller *Coleomegilla maculata* or *Propylea japonica*.

PREDICTIONS FOR EXOTIC AND NATIVE COCCINELLIDS

Based on the scaling rules we calculated species specific values for the critical parameters in the model (consumption rate and basal maintenance rate, together defining reproduction rate). The resulting critical (or equilibrium) prey density, R*, is indicated in Table 1.

These size-related differences in resource utilisation between the various coccinellid species do affect the predictions for invasion and coexistence, as shown in Fig. 4. The higher competitive ability of *A. bipunctata* now shifts the invasion boundary downward, so that *C. septempunctata* is no longer able to invade the system. The same is true for *H. axyridis*. In the latter case *A. bipunctata* is even able to invade a system with *H. axyridis*. In the interaction between *H. axyridis* and *C. septempunctata* it is more clear that *C. septempunctata* should win the competition.

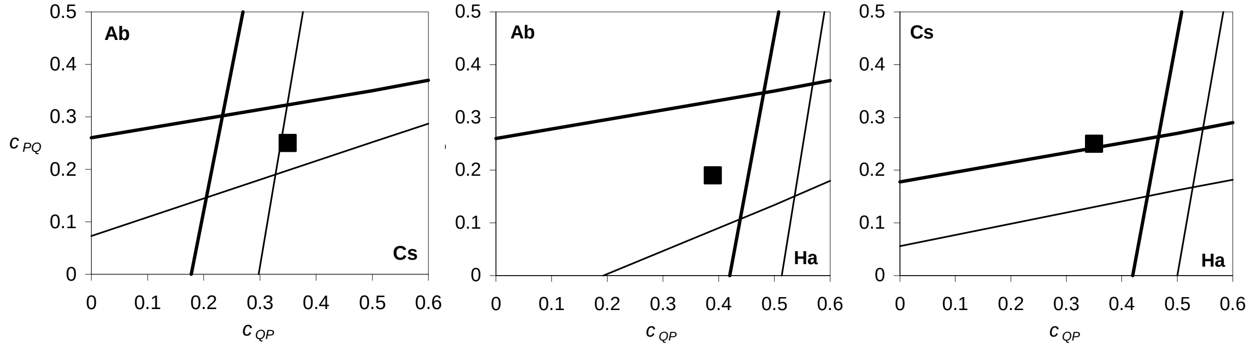

Figure 4. Mutual invasibility plots for specific coccinellid interactions, based on type II functional responses. Thick line indicates the invasion boundaries based on equal competitive abilities; thin line based on the assumption that smaller species are better competitors. Horizontal lines when native species is resident; vertical lines when exotic species is resident. See Table 1 for parameter values.

DISCUSSION

The model approach outlined above should be seen as a first step in analysing the contribution of IGP and ISP to invasion and species coexistence, taking only a few aspects of coccinellid biology into account. More general, however, the analysis shows that knowledge on the asymmetry in IGP is not sufficient to draw conclusions on the ability of a species to invade an existing predator-prey system and to displace the original predator. The level if IGP should, first of all be compared with the level of ISP. When the latter is higher than the former, the level of IGP may be sufficient to invade, but not to replace the other predator. Secondly, competition for common resources may be equally important for the outcome of the interaction. Whereas size generally is an advantage in direct interactions such as IGP, it may be a disadvantage in resource competition. Resource competition, however, can be affected by much more aspects than size, including prey specialisation, habitat dependent foraging efficiency, etc.

ADDITIONAL MECHANISMS FOR COEXISTENCE

Without the impact of resource competition the analysis can be seen as a worst case scenario regarding species replacement, since adding more realism and complexity into that system is likely to increase the likelihood of species coexistence.

SPATIAL AVOIDANCE OF COMPETITION

Intraguild predators may perform behavioural responses that reduces the intraguild interactions. On the other hand, avoidance of intraspecific predation and competition is likely to occur as well. Larval tracks of conspecific ladybirds are known to deter ovipositing females (Yasuda *et al.* 2000). Sibling and kin discrimination by ladybird larvae and females (Joseph *et al.* 1999; Osawa 1992) may reduce ISP as well.

RESOURCE PARTITIONING

All the coccinellid predators and especially the invasive exotics, can feed on a wide range of aphid species, as well as lepidopterans, psyllids, and even pollen (Dixon 2000). Those food ranges, as well as the host plant ranges, may not fully overlap between the different species, which clearly reduces the level of competition, as well as IGP.

TEMPORAL VARIATION

Differences in time of emergence from the overwintering stage may create temporal segregation of resource utilisation. It may, however, also enhance or reverse the asymmetry in competition and IGP, as early arrivals at a resource patch have a headstart in prey depletion, and may benefit from a size advantage in direct intraguild interactions as well (Yasuda *et al.* 2004).

METAPOPULATION DYNAMICS

Finally, asynchrony in prey patch depletion, recreation and recolonisation by predators (as part of a metapopulation process) may provide additional room for coexistence when the best competitor is not the fastest coloniser as well (Osawa 2000).

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