

Intra-host interspecific larval parasitoid competition solved using modelling and bayesian statistics

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ABSTRACT

Intraguild competition is a complex phenomenon that shapes parasitoid communities. When several species of parasitoids oviposit within the same individual host, a complex phenomenon of larval competitive interaction occurs. Within the same guild there is a specialization in competitive strategies, sometimes multiparasitism is avoided, but some species are facultative hyperparasitoids/predators of their competitors.

As these interactions occur within a very small host and during a brief period of time, and that direct observation is very difficult to achieve, we used an alternative methodological approach. We analyzed intraguild host competition mechanisms via the combination of a series of competitive behavioral and functional response models, thurstonian competition model and set theory. These models were fitted via a reversible-jump bayesian model selection procedure to a series of competition experiments data using larvae of three species of *Gonatocerus* spp. (Hymenoptera: Mymaridae), egg parasitoids of the sharpshooter *Tapajosa rubromarginata* (Hemiptera: Cicadellidae) as a case-of-study. This study tests the influence of intrinsic interspecific competition between immature stages within on an individual host, and parasitoid arrival order among the three parasitoid species.

The results showed that the species differed in competitive behavior, some species were better competitors than others. Individuals arriving earlier had a competitive advantage, the weaker species were able to out-compete the stronger ones if the time advantage was longer than 18 h. All the species avoided already parasitized hosts, but in different degrees. The functional response was also different, with the best competitors having shorter estimated handling times. Using this analytical approach on a conventional experimental setup, we gained insights in the mechanism of competition, both on interference and exploitation, and in terms of host selection, all in a single analysis.

1. Introduction

Intraguild competition is a key phenomenon for parasitoid communities (Polis et al., 1989). Most solitary or gregarious endophagous parasitoids require a full host insect to complete their own development (Vinson and Ables, 1980), so, if there are more than one parasitoid species within the same host, a complex phenomenon of competitive interference and predation takes place (Volkoff and Colazza, 1992; Pennacchio and Strand, 2006). Competition between parasitoids can be extrinsic (adult-adult) or intrinsic (adult-larva or larva-larva) (Godfray,

1994).

The analysis of this interaction has two aspects of interest: (1) it helps to understand how parasitoid insect communities are structured and (2) it is important when designing a biological control program, with several controlling species competing with each other. Among the most common difficulties found among studies of competition among parasitoids, are those of observing competition within the host (Harvey et al., 2013). If this is also very small (as in the case of egg parasitoids) and the interactions occur in a very short time, direct observation of this phenomenon is very difficult. Then, complex experimental designs

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and modeling are alternative procedures, being the second option more readily available in the existing infrastructure in the laboratories.

It is known that different species have different competitive strategies, and within the same guild there is a specialization in competition strategies. For example, some species eliminate the competitors via physiological suppression (Chen et al., 2006), other species are facultative hyperparasitoids (Brodeur and Rosenheim, 2000; Hindayana et al., 2001; Lucas, 2005; Cusumano et al., 2011). As a consequence, it has been suggested that interaction between parasitoid guilds should be considered in all biological control programs since competitive effects among them may change the reproductive success of each parasitoid species and thus may affect the host mortality (Nechols et al., 1992; Follett et al., 2000).

Although females of many parasitoid families have the ability to discriminate between unparasitized and parasitized hosts (Wylie, 1965; Van Lenteren, 1981; Ruschioni et al., 2015), in natural systems, multiple species of parasitoids commonly attack the same host (Price, 1971; Hawkins, 1990; Hawkins and Mills, 1996) producing multiparasitism and competition between immature stages (Fisher, 1961; Vinson and Ables, 1980; Cusumano et al., 2011). Multiparasitism occurrence depends on the behavior, reproductive capacity, and phenological synchronization of the female parasitoid with the host (Van Alphen and Visser, 1990; Tumlinson et al., 1993). If the female does not avoid or even prefers a parasitized host, the successful larvae produce adult parasitoids, which changes the population dynamics of the parasitoid species involved and plays a role in sizing and shaping the community (Godfray, 1994).

An interesting approach to analyzing interference competition among parasitoids is the Elo competition model from chess (Elo, 1978) which is already used as a black-box model to analyze animal competitive interactions (Albers and de Vries, 2001; de Vries et al., 2006; Neumann et al., 2011). Intraguild competition between parasitoids may be strongly related to functional response, mostly because the number of hosts attacked depends on the amount available. When there is an excess of hosts, the overlap of different parasitoids within the same host is expected to be less frequent than when their availability is low. If there is an excess of parasitoids, the competition is almost unavoidable. Some authors have combined competition with functional response at population level (Skalski and Gilliam, 2001); and others incorporate interference under intra- and inter-specific competition (de Villemereuil and López-Sepulcre, 2011); yet, no models integrated functional response and behavioral model of the competition process. One problem with these models is their complexity which hinders their analysis. The use of a stepwise model of proposal and selection is a powerful tool to identify the best model that explains a dataset using the fewest parameters possible (Gelman et al., 2003).

Using a novel approach, we analyzed negative interactions between parasitoids (adults and immatures) and their hosts via a series of models, using three egg-parasitoid species as a study-case. For this purpose, we studied the following interactions: indirect extrinsic competition, when two females arrived at the same host at different times regardless of the female detecting if the host was parasitized or not; intrinsic direct competition when a female tried to kill the larvae of other parasitoid species that arrived first to the host; intrinsic direct competition between larvae coming from different species. We conducted black-box laboratory experiments to investigate: (1) the effect of sequential ovipositions of different parasitoid species on the outcome of multiparasitism; (2) the existence of host selection behavior in parasitoid females; (3) the larval competition strength; (4) the effect of interval between ovipositions on the multiparasitism competition outcome. We analyzed the outcome of the experiments by combining functional response models with different variations of the Elo model and set theory.

2. Methods

2.1. Study system

Tapajosa rubromarginata (Signoret) (Cicadellidae: Proconiini), the most frequent and ubiquitous sharpshooter species in Argentina (Paradell et al., 2012), is one of the vectors of the bacteria *Xylella fastidiosa* that causes “Citrus Variegated Chlorosis” (CVC) to Citrus plants (Dellapé and Paradell, 2013). In order to identify biological control candidates to control this vector, we conducted surveys in Argentina between 2003 and 2009, and found 25 species of parasitoid Hymenoptera. During the surveys, we noticed that specimens belonging to three parasitoid families (Mymaridae, Trichogrammatidae, and Aphelinidae) emerged from a single egg mass of *T. rubromarginata*. But the co-emergence of different species of the genus *Gonatocerus*, Mymaridae was more frequent, possibly related to its higher abundance (Logarzo et al., 2004, 2005; Virla et al., 2005, 2009).

2.2. Insect collection and rearing

Laboratory studies were carried out with three egg parasitoids species: *Gonatocerus virlai* (Triapitsyn, Logarzo and de Leon), *G. near tuberculifemur* clade 1, and *G. annulicornis* (Ogloblin) (De León et al., 2008), reared in PROIMI (Planta Piloto de Procesos Industriales Microbiológicos) Laboratory at San Miguel de Tucumán, Tucumán Province. Specimens of *G. virlai* and *G. near tuberculifemur* clade 1 were obtained from egg masses of *T. rubromarginata* collected on Johnson grass (*Sorghum halepense* Pers) in a field at El Manantial (26°49′50.2″S 65°16′59.4″W; elevation 495 m) and San Miguel de Tucumán (26°48′35.7″S 65°16′25.3″W, elevation 470 m) from January to March 2004. *Gonatocerus annulicornis* was obtained from egg masses of the same sharpshooter species on lemon leaves in Horco Molle, Tucumán Province (26°46′50.1″S 65°19′38.3″W; elevation: 703 m) during December 2003. In both areas, parasitoid species were sympatric.

In the laboratory, the colonies were cultured on eggs of *T. rubromarginata* following the methodology established in Virla et al. (2005). Field collected females of *T. rubromarginata* were placed in Polyethylene-Terephthalate (PET) cylindrical vented cages (35 cm high × 18 cm diam.) on lemon plant leaves to obtain host eggs. Potted Citrus lemon plants (pot of 6.3 l) were checked daily for eggs. When egg masses were detected, the sharpshooters and the PET cages were removed, and a leaf with the eggs was ready to be used in the experiments. About 10% of the egg masses were used as control (not parasitized) and maintained until complete development.

All the colonies and the experiments were conducted in the summer at room temperature (26 ± 3°C), at 70–80% RH with natural photoperiod.

2.3. Competition experiment

The experiment consisted of a sequential exposure of leafhopper eggs to parasitoids in an arena which comprised a 10 cm × 1.5 cm culture tube with a cotton plug. An egg mass of *T. rubromarginata* was exposed to the female of one parasitoid species (*G. virlai*, *G. near tuberculifemur* clade 1, or *G. annulicornis*) for 24 hs at the end of which, the female was removed and the egg mass was exposed to a second female of a different species for another 24 hs.

After the second wasp was removed, the exposed egg mass was transferred to a Petri dish with wet tissue paper and covered with clear plastic food wrap to prevent desiccation and to keep wasps from escaping. The egg masses were checked daily and the number of wasps of both species and leafhopper nymphs emerged was recorded. The six possible parasitoid combinations were performed (*G. annulicornis* vs. *G. near tuberculifemur* clade 1; *G. annulicornis* vs. *G. virlai*; *G. near tuberculifemur* clade 1 vs. *G. virlai*, and their reciprocal), 24–58 replicates were conducted (Table 1). As the number of eggs in each egg mass of *T.*

Table 1
Descriptive statistics of the raw data.

Wasp species released		No. egg	No. eggs	Dead eggs	Wasps emerged	Nymphs emerged	Wasps emerged	
First	Second	Masses	Exposed	(%)	(%)	(%)	First (%)	Second (%)
<i>Gnt</i>		81	887	36	54	10	100	–
<i>Ga</i>		81	724	17	77	6	100	–
<i>Gv</i>		90	1368	23	65	2	100	–
<i>Gnt</i>	<i>Ga</i>	11	145	12	71	7	84	16
<i>Ga</i>	<i>Gnt</i>	58	643	6	77	11	38	62
<i>Gnt</i>	<i>Gv</i>	26	234	6	69	15	71	29
<i>Gv</i>	<i>Gnt</i>	24	259	7	74	11	82	18
<i>Ga</i>	<i>Gv</i>	15	139	19	53	0	45	55
<i>Gv</i>	<i>Ga</i>	11	128	8	67	16	84	16

Results of the competition experiment, the species abbreviations are: *G. annulicornis* (*Ga*), *G. virilai* (*Gv*), *G. near tuberculifemur* (*Gnt*). Species are presented in release order. Percentages of dead eggs, wasps emerged, and nymphs emerged were calculated over the total, while percentages of first and second species emerged were calculated over the total of emerged wasps (sixth column).

rubromarginata was highly variable (1–55 eggs each), the egg mass size was used as a random variable and therefore was randomly assigned to all the experiments.

All female parasitoids used in the experiment were 24–48 hs old, mated, with no previous oviposition experience and were used only once. Egg masses used were up to 24 hs old.

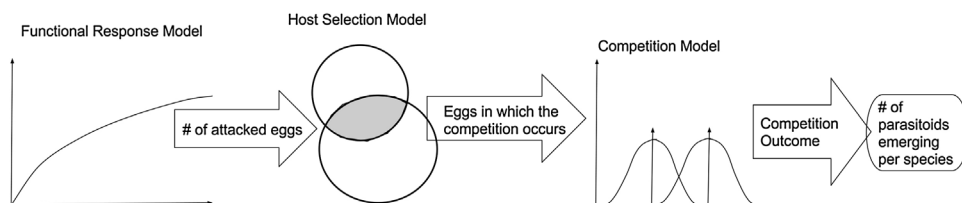
2.4. Functional response estimation

As shown in (Fig. 1), simultaneously to the competition experiment we needed to estimate the number of eggs attacked as a function of eggs offered in the absence of competition (ie: the functional response). The functional response curve was then used as a control to the treatments of consecutive exposures to different parasitoids, this curve also served as a null model in which the absence of interference between hosts was postulated (see section 3.2.1). So, to estimate each species' functional response, an experimental design similar to that explained above was used, with the difference that egg masses were not exposed to a second female. For each parasitoid species, between 81 and 90 *T. rubromarginata* egg masses with a size ranging from one to 55 eggs were used (Table 1).

3. Calculation

The model consists in a succession of three different modules (Fig. 1), a Holling's functional response, a host selection, and a competition model in order to estimate the competition outcome as a function of the number of eggs offered and the order of parasitoid arrival.

As the number of eggs on an egg mass was a random variable, we estimated the number of eggs attacked as a function of eggs offered; consequently, several functional response models were used. On the other hand, we used the Thurstone/Bradley Terry (Thurstone, 1927; Bradley and Terry, 1952) to model the outcome of competition under different conditions. These models are used for creating the Elo rating system in sports (Elo, 1978) that is also used in animal behavior to create dominance ratings between species and/or individuals of the same species (Neumann et al., 2011).



Thurstone (1927). As a result a number of parasitoids from each species is estimated as a function of the number of eggs offered and the order of parasitoid arrival.

We divided the competitive behavior into three dimensions: competitive rating as is used in sports and other animal behavior studies, advantage effect for the first arriving parasitoid, and a host selection behavior as an estimator of the degree of utilization of already parasitized hosts.

After creating the models we performed a stepwise selection of the proposed models in order to find which one had the best balance between explanation of the data (in terms of the likelihood function) and complexity (in terms of number of parameters).

The proposed models are the following:

3.1. Models of functional response

- 1.1- Type I functional response, it is the simplest model, the number of parasitoids emerging from each species is directly proportional to the number of eggs offered (Holling, 1959).
- 1.2- Roger's type II functional response (Rogers, 1972).
- 1.3- Holling's type II functional response.
- 1.4- Holling's Type III functional response.

3.2. Models of competition

3.2.1. Models of functional response without competitive interactions

The functional response models enumerated above were used to test the possible outcome of the experiments under the hypothesis that no competitive interactions occurred.

3.2.2. Models of functional response without host selection behavior

Competition between the parasitoids can be explained as a combination of functional response and a competition for eggs in which both species oviposited. Here the eggs can be classified into four categories: attacked by species a, attacked by species b, not attacked, and attacked by both, as shown in Fig. 2. The expected number of individuals emerged on each experiment as a function of preys (p) was:

$$E_{a/b}(p) = R_a + ((R_a(p) \cap R_b(p))(1 - w_{ab})) \tag{1}$$

where $E_{a/b}(p)$ is the expected number species a emerged, given that species b also attacked the same egg masses, $R_a(p)$ is the functional

Fig. 1. Structure of the model, a functional response model from Holling (1959) estimates the number of attacked eggs by each parasitoid species as a function of the number of eggs offered, followed by a host selection model based on set theory, which estimates the number of eggs in which the competition occurs, finally the competition outcome was estimated using a competition model from

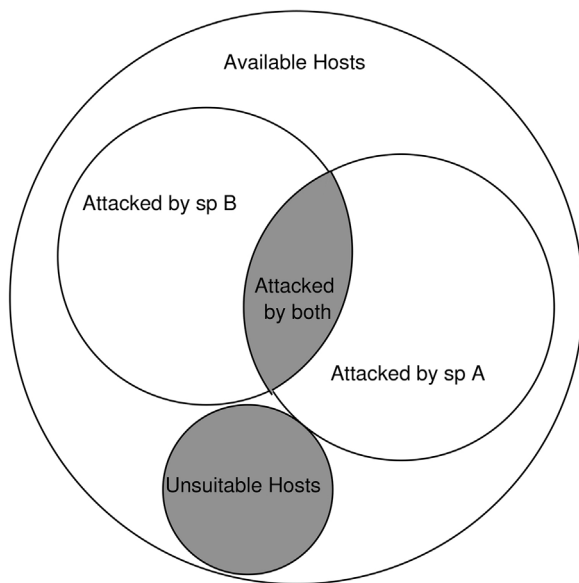


Fig. 2. Venn Diagram showing the four possibilities for the eggs sequentially exposed to both parasitoids. The hosts attacked by parasitoids A and B are subsets of the total eggs offered, the shaded area is the intersection of the subsets A and B, which are the eggs attacked by both parasitoids.

response of species *a*; $R_b(p)$ is the functional response of species *b*, and w_{ab} is the proportion of times in which species *a* won in the competition against species *b*. The number of eggs that was attacked by both species, and the number of eggs in which the competition occurs is assumed to be the product of random superposition and estimated as the product of the proportion of eggs parasitized by *a* and *b* species, multiplied by the total number of eggs offered, which simplifying gives:

$$R_a(p) \cap R_b(p) = R_a(p)R_b(p) \tag{2}$$

where *p* is the total number of eggs offered. On the other hand, the w_{ab} proportion can be calculated according to Thurstone's model case V (Thurstone, 1927) using the following equation:

$$w_{ab} = P(s_a > s_b) \tag{3}$$

where s_a and s_b are the strength in terms of competitive power of species *a* and *b* respectively. $P(s_a > s_b)$ is the proportion of times in which the strength of *a* is superior to strength of *b* (and therefore wins the competition), given that the strength is not a constant number, but a normally distributed random variable.

$$\begin{aligned} s_a &\sim N(\mu_a, \sigma_a) \\ s_b &\sim N(\mu_b, \sigma_b) \end{aligned} \tag{4}$$

thus $P(s_a > s_b)$ is the difference of two Gaussian distributions, so:

$$\begin{aligned} P(a > b) &\sim N(\mu_{ab}, 1) \\ \mu_{ab} &= \mu_a - \mu_b \\ \sigma_{ab}^2 &= \sigma_a^2 + \sigma_b^2 = 1 \end{aligned} \tag{5}$$

where μ_{ab} is the mean competitive strength difference between species *a* and *b*. In Thurstone's case V model $\sigma_a = \sigma_b$, it is possible to assume that $\sigma_a = \sqrt{2}/2$, so $\sigma_a^2 = \sigma_b^2 = 0.5$, so $\sigma_{ab}^2 = 1$, then the expected proportion of times in which *a* overcompetes with *b* within the host is as in Eq. (5).

This model was combined with the models described above, so we obtained another four models with random interference and functional response type I, II (Rogers), II (Holling), and III.

3.2.3. Models of functional response without host selection behavior and advantage for the first arriving host

This is essentially the same series of models as those explained above, but now a constant value is added to the first arriving species in

order to estimate the increase (or decrease) in its competitive strength, so the resulting competitive interaction term of equations (3)–(5) is modified as follows

$$w_{ab} = P(s_a > s_b) \sim N(\mu_a + h_a t - \mu_b, 1) \tag{6}$$

where *t* is the interval in days between the oviposition of the two competing parasitoids, and h_a the first arrival term, which shows the change in competitive strength for the first arriving parasitoid (Hvattum and Arntzen, 2010). If the term is positive, the first arriving parasitoid has an advantage in the competition, and if it is negative, the advantage is for the second species. This term is species-specific. If the term is positive (the first arriving parasitoid has the advantage), the competition is mostly intrinsic (competition between immature stages within the host), meaning that the older/bigger larvae wins. whereas if the term is negative (the second arriving parasitoid has the advantage), the competition might be mostly extrinsic (the female by some means kills the competitor's larvae), meaning that the second female has the opportunity to kill the competitor's larvae in the already parasitized hosts.

3.2.4. Models of functional response with host selection behavior and advantage for the first arriving host

In the series of models explained above, there is an assumption that both female parasitoids choose their hosts at random. So, when the second parasitoid arrives, female host selection is not influenced by whether the eggs were already parasitized or not. This behavior does not necessarily have a biological meaning. It is known that some parasitoids have the ability to discriminate between parasitized and unparasitized hosts (Wylie, 1965; Van Lenteren, 1981), thereby deciding whether to attack parasitized hosts or not. In those cases where multiparasitism succeeds, it becomes a viable strategy (Hamelin et al., 2007). Therefore, we proposed a different host selection model in which we considered different host-selection behavior:

Multiparasitism avoidance The parasitoid avoids already parasitized eggs, so the parasitoid first uses the available “free” hosts, and only after they are completely depleted, does the female use the eggs parasitized by the previous species. So, Eq. (2) can now be modified as:

$$R_a(p) \cap R_b(p) = \begin{cases} R_a(p) + R_b(p) - p, & \text{if } (R_a(p) + R_b(p)) > p \\ 0, & \text{otherwise} \end{cases} \tag{7}$$

Multiparasitism preference The inverse of the avoidance. The parasitoid prefers the parasitized eggs, the female uses these eggs first, and after they are completely depleted, it switches to the “free” hosts. Now the number of eggs attacked by both species follows the equation:

$$R_a(p) \cap R_b(p) = \begin{cases} R_b(p), & \text{if } R_a(p) > R_b(p) \\ R_a(p), & \text{if } R_a(p) \leq R_b(p) \end{cases} \tag{8}$$

Multiparasitism index Since the behavior of avoidance/random/preference is species-specific, the best way to integrate the three models into a single one (and thus avoid the necessity of creating a huge amount of models with all the combinations of behaviors in the studied species), was to create an index of multiparasitism. That index is similar to the correlation coefficient, with a range from 0 to 1; where 0 means complete avoidance, 0.5 means random (without host selection behavior, similar to model 3.2.3), and 1 means complete preference for parasitized eggs. As the index can take intermediate values, the proportion of preference or avoidance vs. random can be averaged. For example, an index of 0.4 means that the estimated number of eggs attacked by both species is a weighted average between random (0.8 weight) and preference (0.2). Also an index of 0.7 is a weighted average in the number of eggs attacked by both species between random (0.4), and avoidance (0.6). So the final equation describing the number of eggs attacked putting together Eqs. (2), (7) and (8) is:

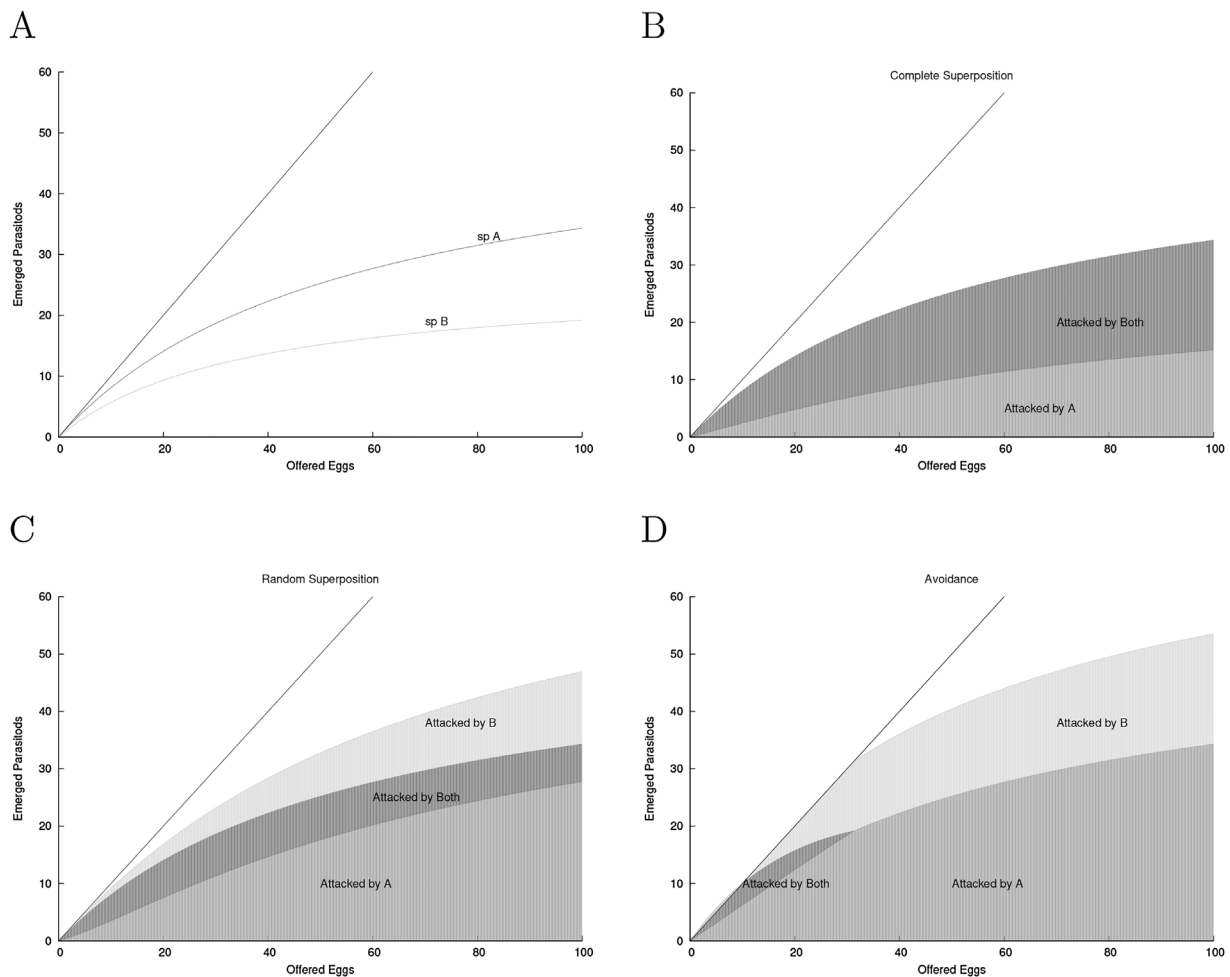


Fig. 3. Expected functional response under different scenarios of interference. (a) Functional response of two species if the eggs are attacked by only one parasitoid, either of species A or B, (b) functional response of a parasitoid, on a host first attacked by species A, under the complete superposition behavior for species B (species B first attacks host already attacked by A), (c) same functional response, but now with random superposition behavior for species B, (d) complete avoidance (species B first attacks hosts not attacked by A).

$$R_a(p) \cap R_b(p) = \begin{cases} N_r(1 - 2i) + N_s 2i & \text{if } i < 0.5 \\ N_r(1 - 2i) + N_a 2i & \text{if } i > 0.5 \\ N_r & \text{otherwise} \end{cases} \quad (9)$$

where i is the multiparasitism index which varies from 0 to 1, N_r is the expected number of hosts attacked by both species under a completely random assumption, as in Eq. (2), N_s is the same variable under complete superposition assumption as in Eq. (8), and N_a is the same variable but now under complete avoidance assumption as in Eq. (7).

The consequences in terms of functional response of these behaviors are shown in Fig. 3a–d. Fig. 3b is a case with complete superposition ($i = 1$), the number of hosts attacked by both species is maximum, Fig. 3c is a case with random superposition ($i = 0.5$), and Fig. 3d is complete avoidance ($i = 0$), where the number of hosts attacked by both species is minimal.

This index translates into a proportion of attacked parasitized or non-parasitized eggs under an excess of hosts, where i is the expected proportion of eggs laid into parasitized hosts, and $1 - i$ is the expected proportion of eggs laid into non-parasitized hosts.

3.2.5. Models of increased mortality/host-feeding

The models described above assumed that the mortality was constant and independent of the number of parasitoids that attacked an egg, that all the eggs were equally suitable, and that the parasitoid does not perform host-feeding. All three phenomena must be taken into

account or they could “flatten” the functional response curve because some hosts are consumed, dead or cannot support the physiological stress of multiple parasitoid attacks and therefore, no parasitoid would emerge from such hosts. That would underestimate the proportion of attacked hosts if the response variable was the number of successfully parasitized hosts as in this study.

Models of increased mortality caused by multiple parasitism A simple parameter of mortality caused by the action of the oviposition of the female was added to test whether the competition between parasitoids caused an increase in the mortality rate of the hosts:

$$E'_{a/b}(p) = E_{a/b}(p)(1 - m)^n \quad (10)$$

where the model from Eq. (1) now has an extra parameter (m) which is the extra mortality caused by the parasitoids and n is the number of parasitoids that attacked a given host. This mortality parameter also includes mortality by host-feeding.

Models with rejection of non-suitable hosts The models described above assumed that all the hosts are considered equally suitable and/or the parasitoid is not able to differentiate between suitable and non-suitable hosts (eggs that do not enable parasitoid development) simple parameter of proportion of not-suitable hosts was therefore added to test whether the presence of that host influences the results:

$$E'_{a/b}(p) = E_{a/b}(p)(1 - s) \quad (11)$$

where the model from Eq. (1) now has an extra parameter (s) which is

the proportion of hosts considered unsuitable or eaten by the parasitoids.

Models with rejection of non-suitable hosts/host-feeding plus increased mortality caused by multiple parasitism. Finally, a model combining models 3 and 4 was also tested:

$$E'_{a/b}(p) = E_{a/b}(p)(1 - s)(1 - m)^n \tag{12}$$

3.3. Model fitting and selection

All the proposed models were used for a stepwise Bayesian model selection, instead of fitting a model and then calculating an information index (such as AIC, DIC, or BIC), we performed the model selection procedure using the algorithm “Reversible Jump Markov-Chain Monte Carlo” in which the routine automatically “jumped” from one model to another and then selected the best model balancing information and fitting. To achieve this, in each jump, for each additional parameter the log-likelihood function was penalized with a value of minus two. This procedure produces better results in cases in which there are “ties” in the above mentioned indexes, and its results are ready to be used in model averaging.

The first 40,000 iterations of the reversible procedure were discarded as a burn-in model selection, and the last 20,000 were used to calculate the weight of each model in the model averaging procedure. Also 1000 iterations of Markov Chain Monte Carlo were performed for each iteration of the Reversible Jump algorithm (Gelman et al., 2003), resulting in a total of 60,000,000 iterations. The last 20,000,000 iterations were used to calculate the *a posteriori* distributions of the parameters.

Expected vs. observed values were compared using a binomial likelihood function for the number of the parasitoids emerged in relation to the total offered. The *a priori* distribution of the parameters of the functional response curves were non-informative uniform distribution between 0 and 1, the same for the multiparasitism index. On the other hand, for the competition parameters, the *a priori* distribution was a normal distribution with mean zero and deviance ten for all the parameters since we did not have a priori information of the variables distribution. Because the competitive strength is an “interval scale” and therefore does not have an origin ordinate (Stevens, 1946), that variable of the species *G. annulicornis*, was arbitrarily fixed as 0 and used as a reference of the competitive strength of the others (so the ordinate of origin was the *G. annulicornis* strength, and the interval unit the standard deviation of that species’ strength). On the selected models, convergence was tested using Geweke plots and visual inspections of the variable traces (Geweke et al., 1991; Gelman et al., 2003). All analysis were performed using a PyMC library for Bayesian estimation (Patil et al., 2010) in the Python programming language.

4. Results

The results of the laboratory competition experiments without fitting the models are shown in Table 1. From the 64 tested models, six models were selected depending on the DIC value and model complexity (Table 2). These integrated models comprise between 15–19 parameters that explain the insect behavior. All the models selected indicated that the species competed among themselves. When the components of the six selected models were analyzed, we found that in terms of functional response, the models with Holling’s type II functional response were the most frequently selected with 69.15% of the iterations, and the models with type III functional response were the remaining 30.85% (Table 2). Therefore, as both models of functional response were selected it is possible that the studied species had a functional response which was neither type II nor type III, instead it could be something in between, but closer to type II as shown in Fig. 4a–c.

Regarding competition models, those that incorporated host

Table 2
Number of parameters for all the proposed models.

Functional Response Models	Models With Increased Mortality	Competition models				With rejection of non-suitable hosts				With rejection of non-suitable hosts			
		Without Competition		With Competition		Without Selection Behavior		With Selection Behavior		Without Selection Behavior		With Selection Behavior	
		Without Competition	With Competition	Without Selection Behavior	With Selection Behavior	Without Selection Behavior	With Selection Behavior	Without Selection Behavior	With Selection Behavior	Without Selection Behavior	With Selection Behavior		
FR1	Absent (Mortality remain constant	3	5	8	11	4	6	9	12	4	6	9	12
FR2 Rogers	and independent of the number of eggs laid in a given host)	6	8	11	14	7	9	12	15	7	9	12	15
FR2 Holling		6	8	11	14	7	9	12	15	7	9	12	15
FR3		9	11	14	17	10	12	15	18	10	12	15	18
FR1	Present (Mortality increase with the number of eggs laid in a given host)	4	6	9	12	5	7	10	13	5	7	10	13
FR2 Rogers		7	9	12	15	8	10	13	16	8	10	13	16
FR2 Holling		7	9	12	15	8	10	13	16	8	10	13	16
FR3		10	12	15	18	11	13	16	19	11	13	16	19

Table of the proposed models, with the combinations of models tested resulting in 64 different models. Values are the number of parameters of each model combination, in bold and parenthesis the weight of the selected models for model averaging after 20,000 reversible jump iterations.

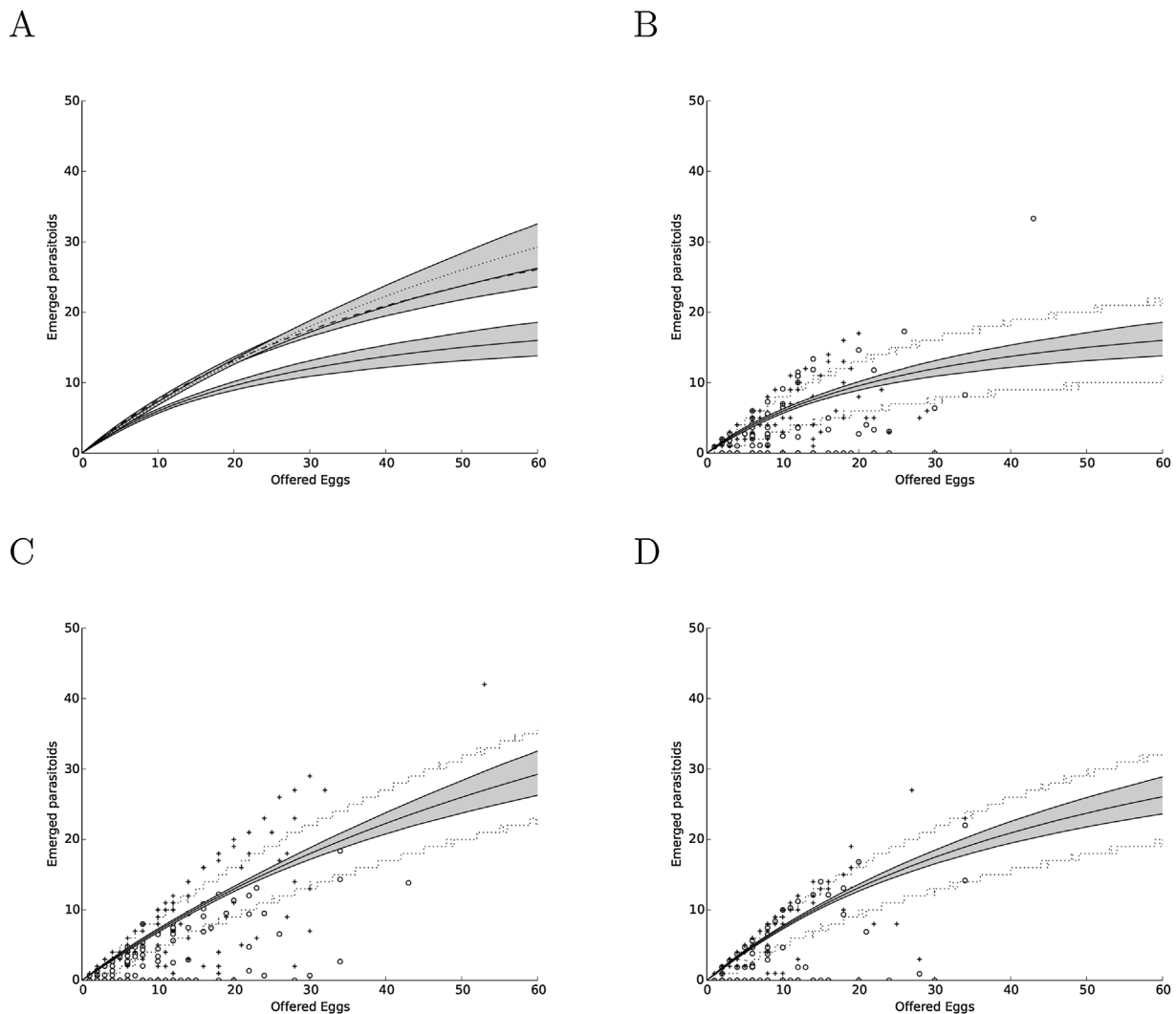


Fig. 4. Observed functional response of the three species. a – functional response of three species together, in the same plot b – functional response of *G. annulicornis*, c – the same for *G. near tuberculifemur*, d – functional response of *G. virlai*. Solid line indicates the mean estimation of functional response, and grey areas indicates its credibility interval. Dashed line indicate the a posteriori credibility interval for individual measurements; open circles are the observed number of emerged parasitoids in competition experiments, while plus signs are the parasitoids emerged from functional response experiments without competition.

selection behavior and advantage for the first arriving host were selected in 100% of the iterations.

In reference to the models of increased mortality caused by multi-parasitism, they were selected in 37.79% of the iterations. This result suggests that the hosts die as a direct effect of the parasitoid attack, and that the increase in mortality was 0.0617 ± 0.033 in the first attack, and 0.1196 ± 0.037 in the second attack regardless if they were attacked by one or two different females. During the study we did not observe host-feeding in any of the parasitoids studied.

Also, some models with rejection of non-suitable hosts were selected in 78.91% of the iterations. This result indicates that some proportion of 0.1851 ± 0.0506 (between 1/5 and 1/6) of the hosts offered were rejected by all the species of parasitoids.

The parameters of the models calculated from the iterations are shown in Table 3. The parameters from the functional response models were similar in both kinds of response type; *G. virlai* was the most efficient, and *G. near tuberculifemur* the least efficient, although the differences were small. In terms of manipulation time, *G. near tuberculifemur* was the fastest and, and *G. annulicornis*, the slowest. All three functional responses are shown together in Fig. 4a. *Gonatocerus virlai* is the most effective species with host densities below 60, and above that number, *G. near tuberculifemur* is superior, *G. near tuberculifemur* is also

the least effective in lower prey densities.

In terms of competitive power, *G. near tuberculifemur* was the strongest, and the weakest was *G. annulicornis*. Using the Thurstone model with the parameters in Table 3, it is possible to infer the proportion of times in which each species wins if arriving simultaneously, with a proportion of 0.3266–0.6734 for *G. annulicornis* vs. *G. virlai* respectively, 0.1791–0.8209 for *G. annulicornis* vs. *G. near tuberculifemur*, and finally 0.3194–0.6806 for *G. virlai* vs. *G. near tuberculifemur*. There was an inverse relationship between competitive power and manipulation time, the fastest attacking species was also the strongest one (Table 3).

All the species have an enormous advantage when arriving first to the host, and after 24 h the weakest species was almost as strong as the strongest. *Gonatocerus annulicornis* was able to win a proportion of 0.5518 and 0.3673 against *G. virlai* and *G. near tuberculifemur* respectively if arriving 24 h earlier. On the other hand, *G. virlai* was the species which benefited most from being the first to arrive, with an increase in strength of nearly two standard deviations (Table 3), now that species was able to win an estimated proportion of 0.9707 and 0.8578 against *G. annulicornis* and *G. near tuberculifemur* respectively. Finally, *G. near tuberculifemur* was the least benefited if it arrived first, nevertheless, its advantage was important (about a half of standard

Table 3
Parameters calculated for the selected models.

Species	Functional response model				Competition model			Multiple parasitism index
	FR2		FR3		Strength	First arrival term (d^{-1})	Multiple parasitism index	
	a (p^{-1})	th (d)	a (p^{-1})	c (p^{-1})				
<i>G. annulicornis</i>	0.9058 ± 0.0577	0.0423 ± 0.0057	0.8618 ± 0.0547	0.0016 ± 0.0012	0 ± 0	0.8198 ± 0.4663	0.5369 ± 0.1409	
<i>G. virlai</i>	0.9593 ± 0.0299	0.0124 ± 0.0028	0.9324 ± 0.0290	0.0010 ± 0.0008	0.6355 ± 0.4665	2.1780 ± 0.4366	0.3307 ± 0.2307	
<i>G. near tuberculifemur</i>	0.8133 ± 0.0485	0.0090 ± 0.0030	0.7885 ± 0.0438	0.0019 ± 0.0012	1.2993 ± 0.4527	0.7411 ± 0.4257	0.8045 ± 0.1516	

A posteriori mean ± standard deviation of the species-specific parameters of the selected models. Parameters reported for the competition term are averaged considering all the iterations with the functional response type II or III together. On the other hand, the functional response parameters were not mixed because even if the common parameters (a and th) had the same meaning in both cases, the values and their behavior were slightly different depending on the type of functional response. Physical units of the calculated parameters, where p is the number of preys, and d days, parameters without units are dimensionless. Other parameters not included in this table were not species-specific (see text).

deviation in strength), and because it was also the strongest competitive species, it was able to win a proportion of 0.9255 and 0.8397 against *G. annulicornis* and *G. virlai* respectively.

5. Discussion

Usually biological control candidates are evaluated using either their functional response parameters or their competitive behavior, but never both together in the same study (de Villemereuil and López-Sepulcre, 2011). Our results showed that the three parasitoid species larvae interacted negatively, affecting their survival when they coexisted regardless of the sequence of exposure of parasitoids and the differences in arrival time. The parasitoid species of genus *Gonatocerus* that attack *T. rubromarginata* eggs competed among them, and showed different competition strategies. The studied species differed in terms of competitive power, advantage of the first to arrive, and their oviposition behavior with a group of parasitized and non-parasitized eggs, reflecting different host selection behavior. Also, they differed in functional response parameter values, attack rate and manipulation time. In our study, we did not observe host-feeding on any of the three parasitoids. For this reason, the mortality increase caused by multiple parasitism is the consequence of the female stings for oviposition and not for feeding (Table 2).

As many parasitoid species (Hubbard et al., 1987; Outreman et al., 2001; Castillo et al., 2004), *G. virlai*, *G. near tuberculifemur*, and *G. annulicornis*, showed a host-discrimination ability and different behaviors regarding multiple parasitism; they were able to differentiate non-viable hosts, and eggs which had already been parasitized. We found asymmetric interference-type of competitive interaction among the studied species (some species were better competitors than others) as in Mahmoud and Lim (2008). *Gonatocerus annulicornis*, the weakest species, was expected to avoid parasitized hosts which could hinder its competitiveness, however, this species did not have a host selection behavior. A possible explanation might be that avoidance of multiple parasitism depends on some other factors, such as the physiological state of the parasitoid, like egg-load and life expectancy, which are mainly determined by a balance between egg and time limitation (Siroto et al., 1997). Also multiple parasitism avoidance is a subject of learning, and therefore can change during the parasitoid lifetime (Hubbard et al., 1999), by using naive females we avoided the learning effect. Another factor that produces multiple parasitism avoidance can be the presence of some viruses (Reynolds and Hardy, 2004). As in Hubbard and Cook (1978) *G. near tuberculifemur*, the strongest species, preferred to use parasitized eggs, behaving like a facultative hyperparasitoid, while *G. virlai* who presented the greatest advantage by arriving first to the host tended to avoid using parasitized eggs.

In terms of functional response parameters, the less aggressive competitor is expected to be the most efficient consumer ($>$ attack rate, and/or $<$ handling time) (Vance, 1985; Fellers, 1987), interestingly the best competitor, *G. near tuberculifemur* species also had the shortest manipulation times. On the other hand, *Gonatocerus virlai* was the species that had the highest attack rate, while *G. annulicornis*, had the longest manipulation time, and a high attack rate, a pattern that is congruent with Abrams (1980), who postulated that in systems with type-2 functional response, negative correlations between handling time and attack rate, result in a reduced level of competition in the community. *Gonatocerus annulicornis*, compensate its reduced competitive ability with a higher attack rate but not with a faster prey manipulation. Therefore, this species might be the best at lower prey densities, and perhaps the best discovering hosts in the field. The advantage of arriving first (expressed in $days^{-1}$) almost compensates the difference in competitive power between the strongest and weakest species (*G. annulicornis* and *G. near tuberculifemur*) from one day to the next.

Considering that the difference in strength of two species that are within the same host is zero, the probability of winning of each species

is 50%. The female behavior of attacking an already parasitized host is meaningful only if the strength of the second arriving species is higher than the species whose larva is already inside the host (Strand and Godfray, 1989). But as the time passes, the first arriving parasitoid increases its strength, until it is more capable from a competitive point of view than any of the species arriving later (Strand and Godfray, 1989; Viser, 1993). So, there is a “window of opportunity” which is the average time in which the first arriving species equals the strength of the second species:

$$0 = s_b + h_b t - s_a \quad (13)$$

$$t = s_a + s_b h_b \quad (14)$$

Therefore, using the values provided by Table 3, it is possible to calculate that window of opportunity, for example for *G. near tuberculifemur* to successfully attack an egg already parasitized by *G. virlai* the time window in hours is 0.3 days or 7 h 19 m. On the other hand, if the egg was parasitized by a *G. annulicornis* the window is now 1.58 days or 38 h 2 m, finally the window of opportunity for *G. virlai* against *G. annulicornis* is 18 h 36 m. These results coincide with field observations in which the eggs are attacked mostly the same day they were laid (Virla, unpublished data). Since these species are purely diurnal, a window of opportunity over twelve hours, means the whole day.

We also found using this approach that the multiparasitism increases the death probability of the host, as it was observed in other parasitoids (Steiner and Piek, 1986; Bernardo et al., 2006). Another female behavior found was the parasitoid rejection of unsuitable hosts as postulated by Godfray (1994).

We developed a series of models which describe the competition process of a community of endoparasitoids at a behavioral level in a comprehensive way. These models provide insights beyond those expected by a conventional setup consisting in a factorial experiment and its corresponding parametric data analysis. We gained insights in the mechanism of competition, both on interference (which species is a better interference competitor, if the competitor has an advantage by arriving first, and if arriving second, whether the parasitoid avoided or not the already parasitized hosts given that arriving first gave it enormous competitive advantage), and exploitation (if there are differences in terms of functional response between species of different fighting strength). All in a single analysis.

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