



A simulation-based method to compare the pest suppression potential of predators: A case study with spiders

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ABSTRACT

Assessing and comparing the pest killing capacity of predators is a crucial but laborious task during the implementation of sustainable farming systems. Critical attributes of assessment include quantifying predator's attack rate (a) and handling time (T_h). The maximum attack rate (T/T_h) (i.e. the maximum number of prey that can be attacked by a predator during the time interval (T) considered) could be a more precise and interpretable indicator of the potential suppression of pests exerted by a predator; however, its calculation only provides a point estimator usually derived from incomplete datasets (e.g. unbalanced or low replicated experimental designs) that could lead to draw wrong conclusions. We introduce **simaR** (simulation of maximum attack rates using R), an R library that generates 95% confidence intervals around estimates of the maximum attack rate that can be easily and intuitively used to compare across species. We validated the simulation method and used the empirical results of a controlled laboratory experiment to compare the maximum attack rates of spiders across a range of Medfly prey densities and illustrate how to use **simaR** with non-replicated partial data. Applying our method we found a significant effect of temperature on the maximum attack rate of two different guilds of spiders, the orb-weaver *A. cucurbitina* and the ambusher *S. globosum* that was not relevant regarding their attack rate and handling time. Our method compares different predator species and/or experimental conditions in a simple and reproducible procedure through an accurate, easy-to-use, fast and statistically robust analysis, based on simulation and bootstrapping, that can be used to assess the pest suppression potential of predators by simulating their functional responses from low-effort laboratory trials.

1. Introduction

A classic way of characterizing the predation behavior of a species in terms of prey consumption is through modeling its functional response, i.e. the number of prey consumed or killed by a predator as a function of prey density (Bolker, 2007; Holling, 1959; Solomon, 1949). Predation can be a critical factor affecting prey population dynamics of pest species, thus its accurate description is crucial for practical and applied aspects of biological control (Van Leeuwen et al., 2007).

The attack rate (a) and handling time (T_h) are the most common parameters obtained from the functional response models and are widely used to compare the efficiency of a predator species as a natural enemy, or how such an efficiency is affected by differing variables (e.g. Dinis et al., 2016; Gilioli et al., 2005; Pasandideh et al., 2015; Tello Mercado et al., 2017). However, variation within these two parameters

can be difficult to interpret in terms of bioecology since they are estimated non-independently of each other. Also, the amount of overlap of their corresponding dispersion measures or interval estimates (e.g. standard deviation and confidence interval) may conceal important ecological patterns only due to low quality datasets (i.e. low replicated and/or incomplete datasets). This fact could lead to misinterpretation of results and affect decision making, for example, selecting a predator as the most efficient against a pest or assessing the effects of a pesticide on the mortality of a selected predator species.

The maximum attack rate (T/T_h), which is the maximum number of prey that can be attacked by a predator or a parasitoid during an interval of time, is a parameter easily calculated using the time interval considered (T) of a functional response experiment and the estimated handling time (T_h) obtained from modeling the functional response of a predator. This measure also allows evaluating the suppression potential

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of a species and it could be used as a stand-alone parameter to make comparisons within a pest control framework since it is directly related to the number of prey killed. However, most published works describe non-replicated experiments and the modeling of a single functional response dataset generates a single point estimator for the maximum attack rate lacking any dispersion measure (e.g. a laboratory experiment conducted during 24 h and an estimated handling time of 1.5 h, gives a maximum attack rate of $24/1.5 = 16$ prey/day). Accordingly, providing a point estimator without a mean and its dispersion measure reduces its usefulness, especially when comparing experiments with a different x and y scales. In fact, in many published works the maximum attack rate is calculated without any dispersion measure or is compared using statistical techniques available from expensive software packages which may limit the number of researchers that could have access to them (e.g. Ahn et al., 2010; Dinis et al., 2016; Mercado et al., 2017).

Simulation based methods have been widely used by ecologists and the number of packages, code and data have been constantly increasing (e.g. Delmas et al., 2017; Réjou-Méchain et al., 2017). Also, within the context of functional response analysis useful tools have been already developed to help estimate the parameters derived from a functional response experiment such as the “frair” package (Pritchard, 2017) for R software (R Core Team, 2016). However, a simulation method to assess and compare directly (e.g. through the maximum attack rate) the potential of different species as natural enemies is still lacking. In addition, the laboratory trials necessary to model a functional response are usually arduous and time consuming because of the difficulty of rearing not only a particular species (e.g. species strongly linked to ecological processes hard to reproduce in laboratory) but also the necessary number of individuals to perform the experiment. This can result in a low number of samples, replicates, or incomplete datasets (e.g. a low number of initial prey densities) that usually causes poor data fitting to the functional response models.

The objectives of this work were (1) to develop a simulation-based method to assess the predatory potential of a species based on the comparison of the maximum attack rate, (2) validate the method, (3) provide an R library to apply the method, and (4) apply the method to two generalist predators fed with a cosmopolitan pest at three temperatures using empirical data as starting point.

Globally, spiders are among the most abundant predators, and their ubiquitous feeding habits upon invertebrate prey qualify them as potential pest control agents in agroecosystems (Benhadi-Marín et al., 2016). The generalist predators selected as model species to apply our method were *Araniella cucurbitina* (Clerck) (Araneae: Araneidae) and *Synema globosum* (Fabricius) (Araneae: Thomisidae). The distribution of *A. cucurbitina* ranges from Europe, Turkey, Central Asia to China and Korea (Nentwig et al., 2018). *A. cucurbitina* is an orb-weaver spider that uses its orbicular web to hunt on trees, bushes and the herbaceous strata (body length male: 3.5 – 4.5 mm; body length female: 4.5–9.5 mm) (Nentwig et al., 2018). *S. globosum* is a palearctic ambusher spider (body length male: 4 mm; body length female: 6.8–8 mm) (Nentwig et al., 2018). Females can be easily observed on flowers, during the day, hunting insect pollinators (Ajuria and Reader, 2014). The selected prey species model was *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae). *C. capitata*, the Mediterranean fruit fly, is a worldwide distributed harmful pest that attacks more than 250 species and affects economically relevant fruit crops such as apple, citrus, figs, peach and pear (Carroll et al., 2002; Weldon et al., 2016).

2. Material and methods

2.1. Origin and rearing of organisms

Subadult spider females of *S. globosum* were individually hand captured from the flowers of *Cistus ladanifer* L. located in Cedães (41° 29' 17" N; 7° 07' 31" W), northeast of Portugal, in early May 2016. Subadults of *A. cucurbitina* were captured by inspecting low size pine

trees around Bragança (41° 50' 19" N; 6° 44' 49" O), northeast of Portugal, during the night in early April 2016.

The spiders were transported into the laboratory in perforated plastic tubes (volume 15 mL). Afterwards, they were transferred individually into plastic Petri dishes (5.2 cm in diameter and 1.2 cm height) and maintained in a climate chamber at $21 \pm 1^\circ\text{C}$, $70 \pm 5\%$ relative humidity and a photoperiod of 16:8 (L:D) h. Every week, half of a 2 cm sphere of sodium acrylate hydrogel was placed on the bottom of each Petri dish to provide water. Spiders were fed *ad libitum* to maturity with adults of *C. capitata* obtained from laboratory cultures maintained at the School of Agriculture of the Polytechnic Institute of Bragança since 2012 (Dinis et al., 2016).

2.2. Experimental arenas

Adult spiders were transferred into plastic cages (7.7 cm in diameter and 4.3 cm height) and starved for 7 days. For *A. cucurbitina* no other elements were introduced in the arena since the spiders build their orb-web under the glass Petri dish top. In the case of *S. globosum* a paper-board strip folded in three parts (S-shaped) was placed in the center of each cage to simulate a flower for shelter. The first part (2 cm × 2 cm) was adhered horizontally to the cage base, the second part (2 cm in width and 3 cm in height) left vertically to the former and acted as stem, and the third one (2 cm × 2 cm) left horizontally the second one acting as flower. Each cage was covered with a glass Petri dish top (9 cm in diameter) and was used as arena. A hole (1 cm in diameter) was opened in the side of each cage and sealed with a cotton ball to facilitate the introduction of prey.

2.3. Functional response assay

Four arenas, one spider per arena, and four initial prey densities ($N_0 = 3, 5, 10$ and 40) were used to assess the functional response of *A. cucurbitina* and *S. globosum* on adults of *C. capitata*. Each of the four spiders was used once (i.e. one replicate) per prey density and temperature giving a total of four individuals × four prey densities × three temperatures = 48 individuals per species. Assays were conducted at three different, but constant temperatures (21°C , 24°C and 27°C) at $70 \pm 5\%$ relative humidity and a photoperiod of 16:8 (L:D) h. For the temperatures 24°C and 27°C the spiders were subjected to an acclimatization period of 7 days, and in all cases, a 7 days period of starvation preceded the functional response experiment. The flies were anesthetized to facilitate manipulation by exposing them to diethyl ether (Panreac, Barcelona, Spain) for 20 s before being transferred into the arenas (once in the arenas, flies recovered their activity behaving normally after 5 min in average). After 24 h, the number of flies killed was recorded.

2.4. Data analysis

2.4.1. Functional response analyses

Statistical analyses were performed using R software (R Core Team, 2016) and were based on the tools available from the “frair” package (Pritchard, 2017). For each dataset (empirical or simulated) we proceed to select the type of functional response in four steps:

Firstly, we fitted the number of prey killed during the time of the experiment to a generic type-I functional response model (a linear increase in attack rate with greater prey density) as:

$$N_e \sim a \times N_0 \times T \quad (1)$$

where N_e represents the number of prey killed, N_0 represents the initial prey density, a represents the attack rate (searching efficiency per time), and T the time of the experiment. For the datasets that did not fit the type-I response we used the *frair_test* function from “frair” package to determine the final shape of the functional response of the remaining cases. The *frair_test* function proceeds by fitting two models by logistic

regression:

$$\text{Killed/not killed} \sim \alpha + \beta \times \text{Density} \quad (2)$$

$$\text{Killed/not killed} \sim \alpha + \beta_1 \times \text{Density} + \beta_2 \times \text{Density}^2 \quad (3)$$

where Density represents the initial prey densities, Killed is the number of prey killed, and not-killed is the difference between them. The function's output provides the sign and *p*-values of the coefficients (β_1 and β_2) used to select between type-II or type-III response.

A negative linear coefficient (β_1) means a better adjustment to type-II functional response (the number of prey killed hyperbolically approaches to an asymptote which represent the maximum attack rate) in which case the most commonly used models are (1) the Holling's type-II predator-prey function (for experiments with prey replacement) (Holling, 1959):

$$N_e \sim (a \times N_0 \times T) / 1 + (a \times N_0 \times T_h) \quad (4)$$

where N_e represents the number of prey killed, a is the attack rate (searching efficiency per time), N_0 is the initial prey density, T is the time of the experiment and T_h is the handling time (time to attack, kill and eat each prey), and (2) the Rogers's type-II decreasing prey function (for experiments without prey replacement, i.e. prey depletion) (Rogers, 1972):

$$N_e \sim N_0 [1 - \exp\{a(N_e \times T_h - T)\}] \quad (5)$$

where N_e represents the number of prey killed, N_0 is the initial prey density, a is the attack rate (searching efficiency per time), T_h is the handling time and T the time of the experiment. The fact that N_e appears in both sides of the equation is due to lacking of prey replacement during the experiment and is solved using the Lambert's transcendental equation (Bolker, 2007).

A positive linear coefficient (β_1) and a negative quadratic coefficient (β_2) imply that the data fit a type-III functional response (the attack rate (a) is a hyperbolic function of prey density) (see Juliano, 2001) in which case a scaling exponent on the attack rate (a) can be implemented as:

$$a \sim b \times N_0^q \quad (6)$$

where a is the attack rate, b is a search coefficient, N_0 is the initial prey density, and as q increases ($q \geq 0$), the functional response becomes progressively sigmoid (Vucic-Pestic et al., 2010). This applies for both the Holling's type-II predator-prey function (i.e. assuming prey replacement) and the Rogers's type-II decreasing prey function (not assuming prey depletion).

Secondly, once the type of functional response (type-II or type-III) was selected, we used the *frair_fit* function to fit the data. The *frair_fit* function fits non-linear predator-prey curves to integer data using the 'Nelder-Mead' method for the selected functional response type estimating its parameters (e.g. attack rate (a) and handling time (T_h)) in the case of a type-II response).

Thirdly, once estimated, the attack rate (a) and handling time (T_h) were bootstrapped using the *frair_boot* function which resamples a previously fitted predator-prey functional response model and provides the 95% confidence intervals for each parameter. The whole empirical confidence interval for each curve was generated using the *drawpoly* function that draws a closed polygon delineated by the upper and lower edges given by *frair_boot* over the plotted curve.

Finally, we calculated the experimental maximum attack rate as T/T_h and proceeded to simulate a series of replicates to generate its confidence interval (see Section 2.4.2).

2.4.2. Simulation for assessing and comparing the prey killing potential of a predator: The *simaR* library

An R library consisting of six core functions was developed to run the whole simulation process (Fig. 1). *simaR* requires a matrix with two columns as input, the first one containing a vector of the initial prey

densities and a second one containing a vector of the proportion of prey killed at each initial prey density. The process described in Fig. 1 is performed by *simaR* once by dataset (in our case study with spiders it is applied six times, one for each of the six species-temperature relationships).

Since each of the prey individual has a certain probability of dying, the pool of discrete data (i.e. the number of prey killed at each initial prey density) is simulated by extracting random values from a binomial distribution with N equal to the total number of available flies and p equal to the proportion of prey that were killed at each initial prey density. By default, a set of 20 simulated samples and 50 datasets (i.e. 50 simulated replicates) is generated for each study case.

Each set of simulated datasets is then passed to the *newTests* function to perform and inspect the test of fitting to a type-II or type-III functional response. Then, the user can select between a series of functional response models already implemented in the "frair" package (see below). The handling time (T_h) can be approximated by the time of the experiment (T) divided by the number of prey killed as $T/N_{e_{max}}$, where $N_{e_{max}}$ is the number of prey killed at the highest prey density (Juliano, 2001) and the mean of this value is used by the next function (*getFitData*) as starting value for the handling time (T_h) to be optimized. By default, the starting value for the attack rate (a) is 0.001.

According to the results of *newTests*, the *getFitData* function allows to select between the following functional response models provided by the "frair" library: (1) Holling's type-II predator-prey function (assuming prey replacement), (2) Rogers's type-II decreasing prey function (not assuming prey replacement), (3) Hassell's original type-III response (assuming prey replacement), (4) Hassell's type-III response (not assuming prey replacement), (5) Scaling exponent response (assuming prey replacement), (6) Scaling exponent response (not assuming prey replacement), and (7) The 'Ecological Models and Data in R' type-II decreasing prey function for more than one predator (assuming prey replacement) (Table S1).

During the former process some outliers could be generated due to the simulation of datasets that poorly fitted the selected functional response model. For example, if the experimental data fit a type-II response and *simData* generates by chance a simulated dataset that fits better a type-I than a type-II functional response, *getFitData* will fit the simulated dataset by brute force (since the response type is selected by the user) as a type-II response. Consequently, the handling time (T_h) for that simulated dataset will be significantly underestimated and accordingly, the value for its estimated maximum attack rate (T/T_h) will be overinflated. The consequence is that the mean of the simulated maximum attack rates may be significantly altered and this bias trespasses to the subsequent bootstrapping process. It is not necessary to inspect the entries in the output of *newTests* one by one, instead, we suggest to check the presence of outliers within the list of simulated maximum attack rates using the *boxplot.stats* function and remove them (if any) manually from the *getFitData* output (that will be passed to *MaxAttackRates*) to ensure accuracy of further calculations.

The simulated curves (50 curves by default according to the number of replicates) can be plotted using the *plotCurves* function to visually inspect the simulation results. Then, the function *MaxAttackRates* calculates the maximum attack rate for each simulated replicate as T/T_h .

Finally, the mean of the simulated maximum attack rates is bootstrapped using the *MARbootstrapping* function that calls the *boot* function from "boot" package running a selected number of bootstrap replicates to generate its 95% confidence intervals.

2.5. Validation of simulation method

The validation of the method was carried according to three objectives: (1) to assess the correspondence between the known (true) maximum attack rate obtained from an artificial dataset and the estimated value provided by *simaR*, as well as the proportion of cases in which the simulated confidence interval provided by *simaR* overlapped

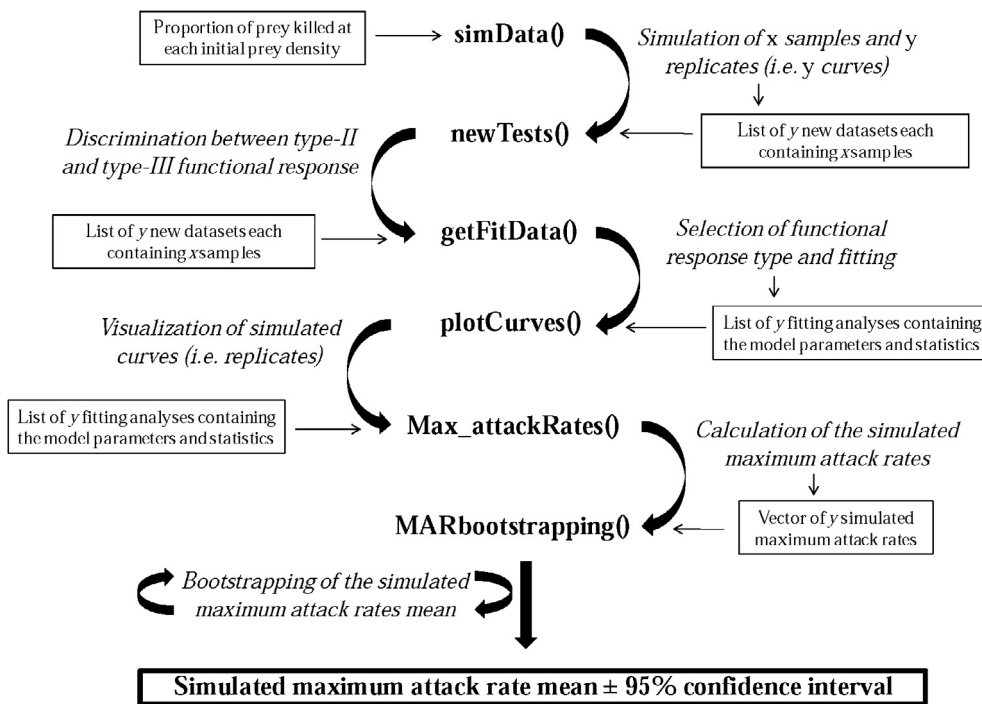


Fig. 1. Workflow with the *simaR* library. The six core functions are shown in bold. The expected input and the output generated by each function are shown in boxes. The processes carried out by each function are shown in italic. In our case study with spiders the whole process was done six times, one for each of the six species-temperature relationships.

the known (true) value, (2) assess the performance of the method using partial data, and (3) assess the correspondence between the maximum attack rate calculated by *simaR* and the point estimator for it obtained from literature across different study cases.

2.5.1. Correspondence between the known and simulated maximum attack rate calculated by *simaR*

Since the maximum attack rate is a point estimate calculated from the handling time, we used an artificial dataset generated from a functional response model with known parameters, and then the parameters were estimated back using *simaR*. For this, we considered 11 initial prey densities ($N_0 = 3, 5, 10, 15, 20, 25, 30, 35, 40, 45$ and 50) assuming prey replacement and their corresponding number of prey killed (N_e) were calculated using the Holling's type-II predator-prey function.

We assigned a time of experiment $T = 24$ h, an attack rate $a = 0.05$, and a handling time $T_h = 1.30$, i.e. a known maximum attack rate T/T_h of $24/1.30 = 18.46$ prey/day, so that the number of prey killed for each initial prey density was $N_e = 3.00, 4.53, 7.27, 9.11, 10.43, 11.43, 12.20, 12.82, 13.33, 13.76$, and 14.12 respectively (Fig. S1A). Then we run 1000 simulations (50 replicates of 20 samples per initial prey density per simulation, i.e. 50.000 simulated datasets) using the *simaR* library to estimate the maximum attack rate, and the number of times the known maximum attack rate fell within the simulated confidence interval was calculated. Finally, a one sample Student's *t*-test was carried out to check if the real maximum attack rate differed significantly from the simulated ones.

2.5.2. Performance of *simaR* on partial data

We considered 11 initial prey densities ($N_0 = 3, 5, 10, 15, 20, 25, 30, 35, 40, 45$ and 50) without assuming prey replacement, assigned a proportion of prey killed for each density ($p_c = 1, 0.9, 0.8, 0.7, 0.6, 0.5, 0.4, 0.3, 0.3, 0.3$ and 0.3), and assumed a time of experiment of $T = 24$ h. Then, we simulated the number of prey killed for each initial prey density by extracting 10 random values (i.e. 10 samples) from a binomial distribution with $N = N_0$ and $p = p_c$. Then, two series of five and six new datasets respectively were created in two ways: the first series by arbitrary removing a number of initial prey densities (N_0) from the complete original simulated dataset keeping constant the number of

samples (i.e. $n = 10$), and the second one by removing the same initial prey densities together with the 50% of the samples (i.e. $n = 5$). We used the *frair.test* function to assess the type of functional response of the original dataset ($N_0 = 11; n = 10$) (Fig. S2A) and its corresponding sample-reduced dataset ($N_0 = 11; n = 5$) (Fig. S2B). For each of the two datasets, the attack rate (a) and handling time (T_h) were estimated using the *frair.fit* function from the “frair” package and the estimated handling time was then used to calculate the empirical maximum attack rates (T/T_h). Finally, the 11 new partial datasets were used together with the original one to apply the simulation method with *simaR* (Figs. S3 and S4).

Ten simulation runs were carried out for each of the 12 datasets (20 samples and 50 replicates per simulation run) and the effect of the simulation run and number of samples ($n = 10$ or $n = 5$) on the simulated maximum attack rate was assessed. We used the Shapiro-Wilk test to check if the simulated data were normally distributed ($W = 0.853$; $P < 0.001$) and then the simulated maximum attack rate was linearly modeled following Zuur et al. (2009) as:

$$\varepsilon_i \sim N(0, \sigma^2)$$

$$SMAR \sim \alpha + \beta_1 \times Run + \beta_2 \times Samples + \beta_3 \times Run \times Samples + \varepsilon_i$$

(7)

where *SMAR* represents the simulated maximum attack rates, *Run* represents the number of simulation run, *Samples* represents the number of samples used at each initial prey density in the original dataset and *Run * Samples* represents the interaction term between the two independent variables.

2.5.3. Correspondence between the *simaR* estimation of the maximum attack rate and point estimators obtained from literature

We searched for papers focused on the functional response of different natural enemies in different conditions (e.g. response of a natural enemy to different temperatures or response of different natural enemies against the same pest) that provided the mean number of prey attacked at different prey densities. We used the proportion of attacked prey to replicate the analyses conducted in the literature using *simaR*, and the simulated maximum attack rates (T/T_h) together with their 95% confidence intervals were generated. Then, in order to check the

correspondence between the simulated maximum attack rates obtained using simaR and the corresponding ones obtained from literature, the latter were linearly modeled as:

$$\varepsilon_i \sim N(0, \sigma^2)$$

$$\text{LiteratureMAR} \sim \alpha + \beta \times \text{simaRMAR} + \varepsilon_i \quad (8)$$

where MAR represents the maximum attack rates.

2.6. Application of the simulation method to experimental data with spiders

We used the “frair” package to select, fit the functional response model, and estimate the corresponding parameters (as described in Section 2.4.1) of each spider-temperature relationship. Then we used the simaR library to simulate and generate the 95% confidence interval (as described in Section 2.4.2), and compare the maximum attack rate of each spider species between the three selected temperatures. A type-I functional response is supposed to be independent from the handling time, which could be considered unrealistic because the consumption rates cannot continue increasing indefinitely regardless of food density. On the other hand, Batzli et al. (1981) argued that after providing the test organism with the highest food densities found in their natural habitat it would be reasonable to conclude that a type-I response can be exhibited. However, this range of higher prey densities in nature could be unknown for the test organism, which is the case of the two selected spider species selected for this work. Because of this, the type-I responses found along this study were fitted as the increasing part of a Rogers's type-II decreasing prey function (i.e. a type-II response that did not reached the asymptote).

3. Results

3.1. Correspondence between the known and estimated maximum attack rate calculated by simaR

The known value for the maximum attack rate of the artificial dataset generated to test the correspondence between the known and the simulated parameter was 18.46 prey/day and the maximum attack rate calculated by 1000 simulation runs using simaR was 18.459 ± 0.003 (mean \pm SE). The lower and upper limit of its simulated 95% confidence interval were 18.274 ± 0.003 (mean \pm SE) and 18.645 ± 0.003 (mean \pm SE) respectively. The known maximum attack rate fell 955 times of 1000 simulation runs within the simulated confidence intervals giving a method accuracy of 95.50% (Table S2) (Fig. S1B) and did not differed significantly from the simulated value ($t = -0.805$, $df = 999$, $P = 0.421$)

3.2. Performance of simaR on partial data

The original complete dataset ($N_0 = 11$; $n = 10$) (Fig. S2A) and the corresponding sample-reduced dataset ($N_0 = 11$; $n = 5$) (Fig. S2B) generated to test the method performance on partial data fitted a type-II functional response ($\beta_1 = -0.0515$; $Z = 15.473$; $P < 0.001$, and $\beta_1 = -0.052$; $Z = -10.982$; $P < 0.001$ respectively). Accordingly, the Rogers's type-II decreasing prey function was fitted for each dataset giving a coefficient of attack rate of $a = 0.148 \pm 0.020$ (estimate \pm SE) ($Z = 7.552$; $P < 0.001$), an estimated handling time of $T_h = 1.68 \pm 0.071$ (estimate \pm SE) ($Z = 23.719$; $P < 0.001$), and an empirical maximum attack rate of (T/T_h) of 14.29 prey/day for the original complete dataset. The sample-reduced dataset ($N_0 = 11$; $n = 5$) generated a coefficient of attack rate (a) of 0.149 ± 0.030 (estimate \pm SE) ($Z = 5.130$; $P < 0.001$), an estimated handling time (T_h) of 1.742 ± 0.105 (estimate \pm SE) ($Z = 16.553$; $P < 0.001$), and an empirical maximum attack rate (T/T_h) of 13.777 prey/day.

The simulated maximum attack rates were 14.23 ± 0.01 (mean \pm SE) and 14.11 ± 0.08 (mean \pm SE) for the pool of datasets

with 10 samples and 5 samples respectively (Table S3). The simulation run number had not a significant effect on the simulated maximum attack rate estimation ($F = 0.779$; $df = 1$; $P = 0.379$) (Fig. S5A). The number of samples (n) of each dataset did not affected significantly the estimation of the parameter ($F = 1.535$; $df = 1$; $P = 0.218$) (Fig. S5B), and the interaction between the two variables was not significantly as well ($F = 0.494$; $df = 1$; $P = 0.484$).

3.3. Correspondence between the simaR estimation of the maximum attack rate and point estimators obtained from literature

Regarding the values for the maximum attack rate extracted from literature, we found six papers focused on the functional response of different groups of natural enemies (seven species of predators and one parasitoid) in different conditions that used three types of functional response to fit the data and that provided the mean of the number of attacked prey at each initial prey density (Table S4). The results reported in these papers were used together with the re-analysis of the functional response data of our previous paper on the pest suppression potential of two species of carabids (Dinis et al., 2016; Table S4). The linear regression carried out between the simulated maximum attack rates obtained using the simaR library on their corresponding bibliographic maximum attack rates gave a coefficient of determination (R^2) of 0.932 (Fig. S6).

3.4. Application of the simulation method to experimental data with spiders

The estimated parameters from the logistic regression analysis of the empirical proportion of *C. capitata* adults killed by adult females of *A. cucurbitina* and *S. globosum* indicated a type-II functional response at each tested temperature except for the former species at 21 °C which showed a type-I functional response (Table 1). The highest number of killed preys was obtained at 21 °C with *A. cucurbitina* (Fig. 2A) whereas the lowest one was observed in *S. globosum* at 21 °C (Fig. 2B). Almost the total of the simulated curves ranged within the empirical confidence intervals of the empirical curves for both *A. cucurbitina* and *S. globosum* (Fig. 3) although the simulated range of curves differed slightly from the empirical one in the case of *A. cucurbitina* at 21 °C (Fig. 3A).

The coefficient of attack rate (a) corresponding to the type-I response of *A. cucurbitina* at 21 °C was the lowest one across the six spider-temperature relationships (Table 1), however it was not significantly different along the gradient of temperature for this species (Fig. 4A). The estimated handling time (T_h) of *A. cucurbitina* was not significantly different between 24 °C and 27 °C (Table 1) (Fig. 4B). The simulated maximum attack rate of *A. cucurbitina* was significantly higher at 21 °C when compared to 24 °C and 27 °C, however, it was not significantly different between the two latter temperatures (Fig. 4C).

In the case of *S. globosum* both the attack rate and handling time decreased across the increasing gradient of temperatures (Table 1). However, based on the overlapping of the 95% confidence intervals, no significant differences in attack rate or handling time could be observed (Fig. 4D and E), except for the handling time at 21 °C and 27 °C where the former was significantly higher than the latter (Fig. 4E). Finally, significant differences between the simulated maximum attack rates among the three temperatures were found for *S. globosum* increasing from 21 °C to 27 °C (Table 1) (Fig. 4F).

4. Discussion

4.1. Method validation and performance

We developed a method to assess the prey killing capacity of a predator which uses the maximum attack rate (T/T_h), a parameter derived from the functional response of a species under selected experimental conditions, to evaluate the capacity of a predator or a parasitoid to attack a number of prey individuals during a given time.

Table 1

Estimated parameters from the linear and logistic regression analysis of the number of prey killed against prey density for the two spider species studied. Estimate: coefficients derived from the logistic regression used to select between type-II and type-III type of functional response; α : coefficients of attack rate and their confidence interval (α CI); T_h : estimated handling times and their confidence interval (T_h CI); MAR: maximum attack rates (T/T_h) of the empirical datasets; mMARs: simulated maximum attack rate means and their confidence intervals (mMARs CI). AC: *Araniella cucurbitina*; SG: *Synema globosum*. E.type: Empirical response type; S.type: simulated response type. Asterisks indicate statistical significance at $p < 0.05$. F indicates the F-value (1 degree of freedom) corresponding to the type-I functional response fitting.

Predator	Temperature	Estimate	Std. Error	Z-value	P	α	α CI	T_h	T_h CI	MAR	mMARs	mMARs CI	E.type	S.type
AC	21 °C	0.5031	0.0267	354.36 ^F	< 0.001 [*]	0.0230	0.0210, 0.0250	–	–	–	86.7388	78.5528, 95.0345	I	II
	24 °C	–0.0439	0.0093	–4.7303	< 0.001 [*]	0.0620	0.0370, 0.0910	1.2820	0.8800, 1.6250	18.7207	18.9839	18.4930, 19.4728	II	II
	27 °C	–0.0333	0.0090	–3.7097	< 0.001 [*]	0.0470	0.0280, 0.0820	1.2820	0.7200, 2.0500	18.7207	19.1139	18.4856, 19.7602	II	II
SG	21 °C	–0.0507	0.0095	–5.3174	< 0.001 [*]	0.0570	0.0440, 0.1000	2.7010	2.1860, 4.1220	8.8856	8.9710	8.6191, 9.3314	II	II
	24 °C	–0.0286	0.0091	–3.1590	0.0016 [*]	0.0370	0.0180, 0.1230	1.5820	0.5760, 6.8580	15.1707	15.7094	15.0262, 16.3917	II	II
	27 °C	–0.0188	0.0088	–2.1363	0.0327 [*]	0.0320	0.0230, 0.0480	0.8040	0.1110, 1.6320	29.8507	31.8333	30.0105, 33.6730	II	II

The development of this method was born from the need to make statistical hypothesis testing using experimental data with a low number of samples, low replicated assays, or even partial data in the context of predator functional response research. We selected the confidence interval method to test hypotheses because of its ability to help quantify the magnitude of an effect in units of scientific interest (Jiroutek et al., 2003).

The way to generate the confidence intervals was through simulation, a method that allows to recreate a selected number of both samples and replicates, followed by bootstrapping that allows to resample data matrices and generate dispersal measures around an estimate (e.g. the mean) at a desired level of confidence (usually 95%). We provided the simaR library that run the whole process using an experimental approximation of the handling time ($T/N_{e_{max}}$) as starting value to parameterize the simulated handling time, which in turn is used to calculate the simulated maximum attack rate and its 95% confidence interval.

It is important to say that the resulting intervals should be proper confidence intervals or at least good approximations (i.e. a 95% confidence interval should overlap the known value with a probability of 95%). Commonly, the true values are not known since the parameter to be simulated and for which we want to provide confidence intervals is an estimate itself (e.g. the handling time). Accordingly, we validated the method by fabricating an artificial dataset with known parameters

and estimated the parameters back reaching an accuracy of 95.50%. Moreover, when testing the performance of the method using partial data, we found consistency on the parameters estimation by simulation, i.e. the maximum attack rate and the lower and upper bound of its confidence interval. This suggest that the effect of gaps in the data can be solved by using a selected number of simulated samples and replicates (in our case 20 and 50 respectively). Also, when only the means of the number of prey killed were available (i.e. bibliographical sources) our method loosed only a 6.80% of information.

When comparing our experimental and simulated data for spiders we also found a good overlap between the simulated range of curves (i.e. replicates) and the experimental data despite a slight difference in the case of *A. cucurbitina* at 21 °C because the fitted models were different, i.e. type-I (empirical) and type-II (simulated).

4.2. Method limitations

In general, our method allows a fast and accurate comparison of the maximum attack rates of different study cases; however, some points have to be stressed. We used the known value of the simulated parameter to validate the method and an *ad-hoc* sample size and number of replicates for simulation (20 and 50 respectively), since a confidence interval that includes the true parameter value may slightly differ from a confidence interval that does not include it (Beal, 1989), further

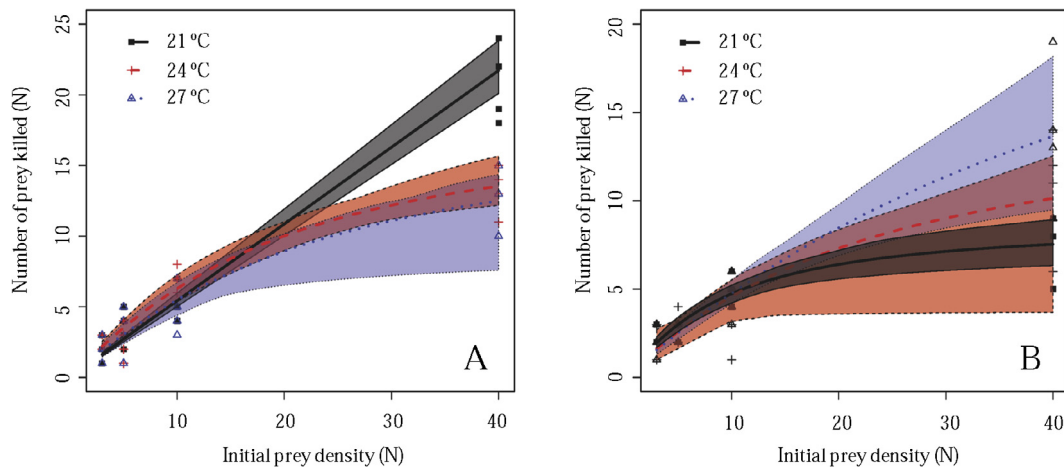


Fig. 2. A: Functional responses of adult females of *Araniella cucurbitina*, and B: *Synema globosum* fed for 24 h on differing densities of adults of *Ceratitis capitata* at three temperatures. Points represent the number of flies killed at each prey density. Thick lines represent the fitted values of empirical data and the polygons that surround them represent the limits of the confidence interval of the empirical curves for each temperature.

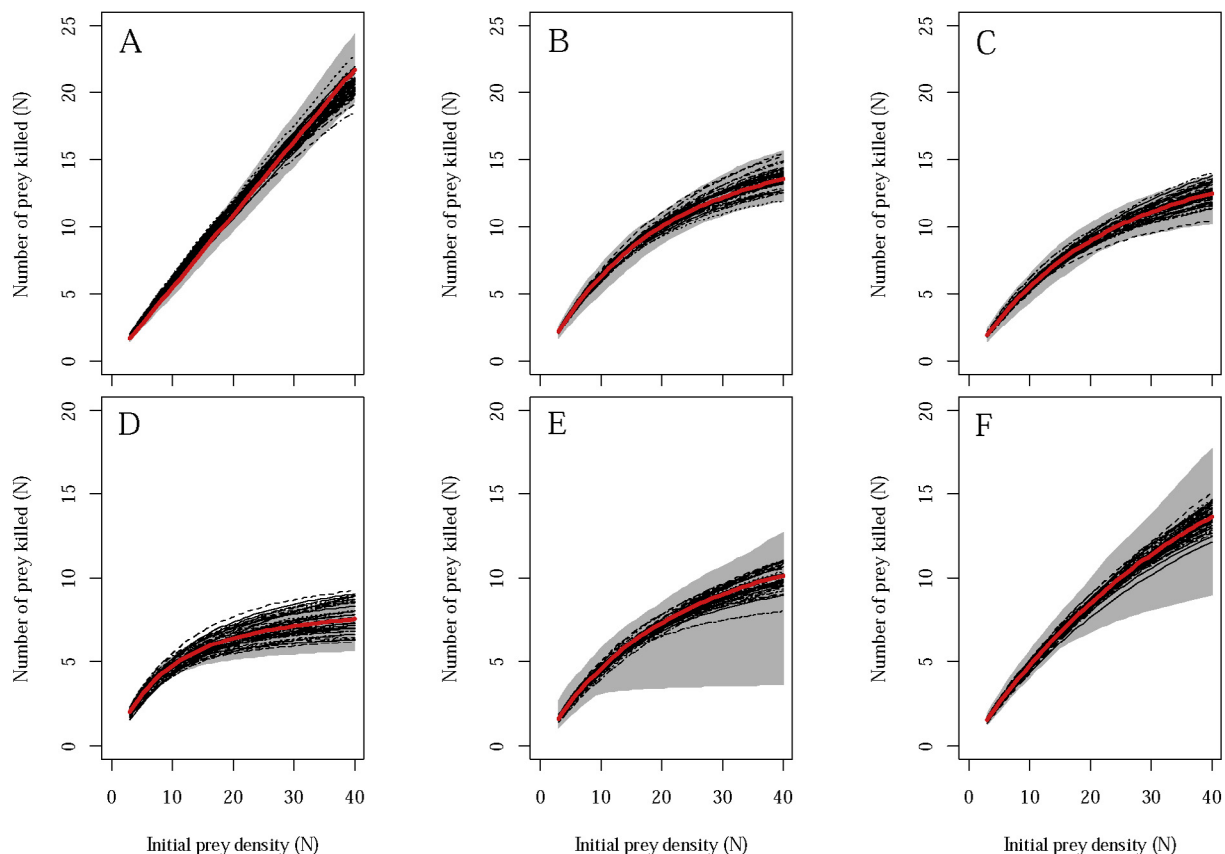


Fig. 3. Comparison between the empirical and simulated functional responses of adult females of *Araniella cucurbitina* (A: 21 °C; B: 24 °C and C: 27 °C) and *Synema globosum* (D: 21 °C; E: 24 °C and F: 27 °C) fed for 24 h on differing densities of adults of *Ceratitis capitata*. The mass of thin lines represent the fitted values of each simulation run using the Rogers's type-II decreasing prey function. Thick lines (red lines) represent the fitted values of empirical data for each temperature. The shaded areas represent the 95% confidence interval obtained using “frair” for each empirical curve (based on 999 bootstrap replicates). Dots were omitted to facilitate visualization. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

combination of simulation runs should be carried out to test in which extent the number of simulated samples and simulated replicates may affect the size of the confidence interval, for example, is a simulation of 20 samples and 50 replicates significantly different from another one of 10 samples and 100 simulations? In which cases such a combination is more accurate and/or appropriate? In addition, extracting random values from the binomial distribution is an approximation and the assumption of independence between the fates of individual prey should be investigated in the future.

We used simulated data to validate the method toward the estimation of a biological parameter such as the maximum attack rate using empirical data. Since no ecological information is represented by the initial artificial dataset beyond the fit to a selected model, it could be argued that the method can be applied to any species under any laboratory conditions that the code allows to select (i.e. time of the experiment, number of predators, prey replacement, and type of functional response). However, conclusions derived from different functional response analyses must be carefully drawn since variation in physical and biological conditions of the studied system such as starvation before the experiment, arena size, and acclimatization period are not taken into account by the model equations and may lead to ecological misinterpretations. For instance, in which extent the conclusions of a laboratorial experiment on functional response can be extrapolated to the field?

Since natural assemblages have multiple prey species that are subjected to seasonal processes, key community-related concepts such as food preference and prey preference (Wise et al., 2006), behavioral differences among conspecifics (Toscano and Griffen, 2014), successional processes (Settle et al., 1996), intraguild competition and prey

availability (Perkins et al., 2018) and predator-prey body size proportion (Shimazaki and Miyashita, 2005) can have implications for ecosystem functioning and stability and should also be considered within the context of functional response modeling.

Finally, the *simaR* library contemplates a type-II decreasing prey function for multiple predators, but multispecies functional response models are not currently included. Nevertheless, development of methods accounting for multiple prey functional responses and predator and prey behavior are of growing interest (e.g. Scharf et al., 2008; Smout et al., 2010). Accordingly, within the context of biological control, further research is needed to test under which situations the parameters of the functional response models and their derivatives such as the maximum attack rate could be suitable stand-alone surrogates of the suppression potential of a biological control agent.

4.3. Bioecological interpretation of the effect of temperature on the spiders functional response

Since temperature is a key driver in pest control, e.g. high temperature usually hinders the natural enemies action in greenhouses (Gilioli et al., 2005; Vacante, 2000), we applied our method to experimental data obtained in the laboratory at different temperatures (21, 24 and 27 °C) on two widespread species of generalist predators, the orb-weaver spider *A. cucurbitina* and the ambusher spider *S. globosum* against the pest *C. capitata*.

The maximum attack rate of *A. cucurbitina* decreased dramatically from 21 °C to 24 °C and was not significantly different from the latter temperature to 27 °C. This reduction in the efficiency of capturing prey according to the temperature by orb-weavers have been well

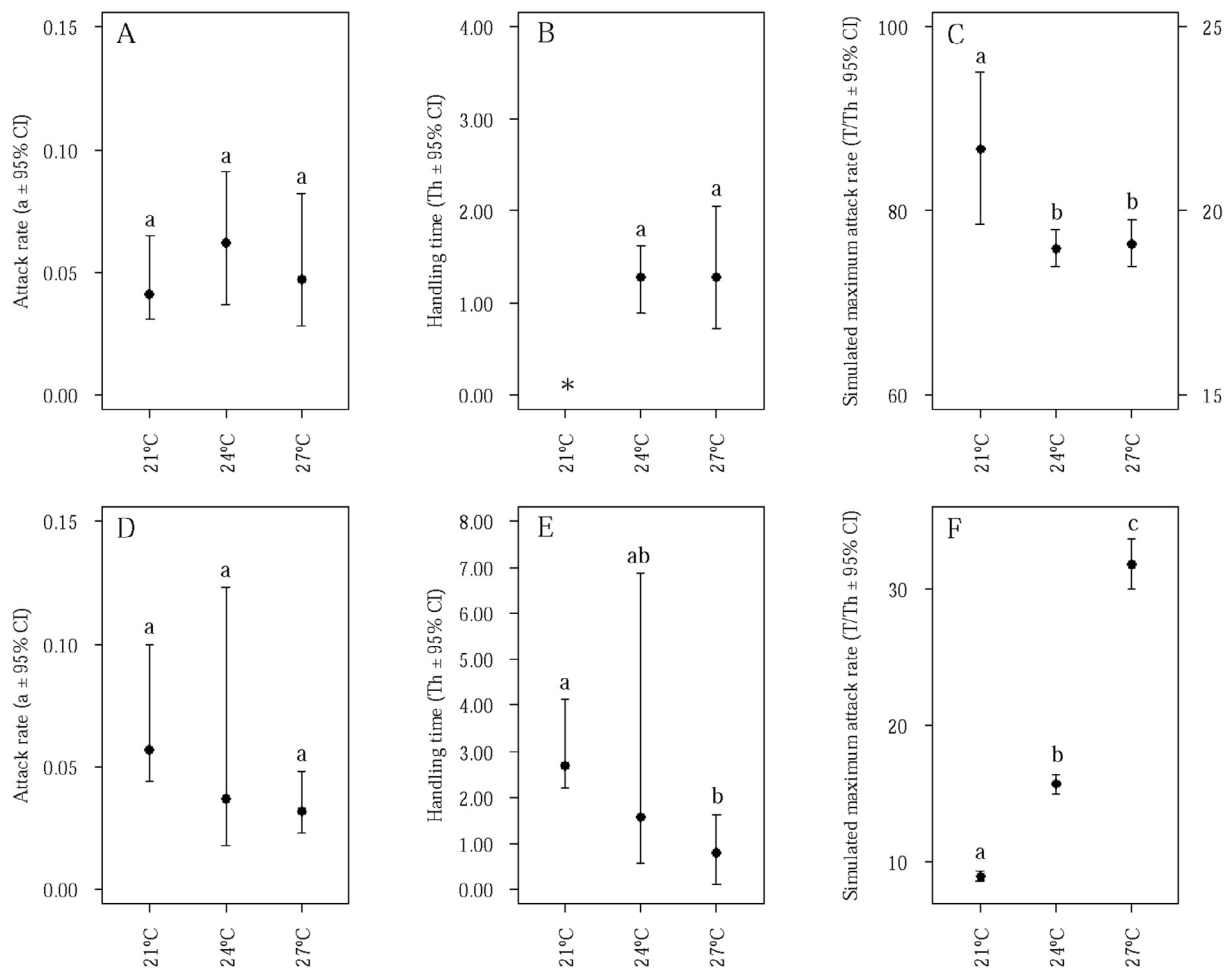


Fig. 4. Parameters of the functional response of adult females of *Araniella cucurbitina* (A: attack rate (a); B: empirical handling time (T_h), and C: maximum attack rate (T/T_h)), and adult females of *Synema globosum* (D: attack rate (a); E: handling time (T_h), and F: maximum attack rate (T/T_h)) fed for 24 h on different densities of adults of *Ceratitis capitata* at three temperatures. Since the scale of the simulated maximum attack rate is very different at 21 °C than at 24 °C and 27 °C, in C the simulated maximum attack rate at 24 °C and 27 °C are represented on the secondary right vertical axis to facilitate visualization. Attack rates and handling times were estimated using the “frair” package and the maximum attack rate was simulated using simaR. Dots represent the original data and bars the 95% confidence intervals given by bootstrapping (999 bootstrap replicates). Different letters over bars indicate significant differences based on the overlap of confidence intervals. *In B, the handling time at 21 °C is empty because the fitted model was of type-I.

documented from different points of view. Hesselberg and Vollrath (2006) performed an experiment with *Araneus diadematus* Clerck (Araneae: Araneidae) against *Drosophila melanogaster* Meigen (Diptera: Drosophilidae) and hypothesized that flying insects had a higher body temperature because of the flight whereas the spiders had a lower body temperature waiting in the centre on their web. In our experiment, this difference in body temperature could make the escape time of *C. capitata* significantly faster at 24 and 27 °C. In addition, the web building architecture of *A. diadematus* was also found to be significantly different at lower temperatures by Vollrath et al., (1997) and suggested that the increase in spiral spacing could be an adaptation to larger sized prey supposedly able to fly at lower temperatures.

Hunting success of orb-weavers relies on their web efficiency. The capture threads of this web are coated with glue droplets composed by an adhesive viscoelastic glycoprotein covered by an aqueous solution. This aqueous glue, plasticizes the silk and provides elasticity from the surface tension of the liquid (Vollrath and Edmonds, 1989). However, environmental changes in temperature have the potential to alter thread and web function, and Stellwagen et al. (2014) found that an increase in temperature decreased the glycoprotein viscosity of the thread build by *Argiope aurantia* Lucas (Araneae: Araneidae). This effect may also alter the mechanical properties of the webs of *A. cucurbitina* significantly decreasing the efficiency in capturing prey at high

temperatures.

Moreover, biomechanical properties of silks and structural diversity of spider webs are highly variable and also depends on rate of spinning, pH levels in the silk glands, humidity and temperature (Harmer et al., 2011). In fact, the dependency of spider webs on environmental and physiological conditions is not exclusive of orb-weavers. Barghusen et al. (1997) suggested that *Achaeanea tepidariorum* C.L. Koch (Araneae: Theridiidae), an aerial space web builder (Uetz et al., 1999) optimizes web construction by temperature selection and found an optimal experimental temperature at 20 °C at which the spiders produced the heaviest webs and prey capture should be maximized.

In our experiment, *S. globosum*, a sit-and-wait active hunter (i.e. ambusher without web device) showed a clear significant increasing pattern of the maximum attack rate from the lowest to the highest temperature tested. This gradient in hunting success could be explained in terms of the effect of temperature in both the predator and the prey. As for orb-weavers, the fact that an ambusher spider waits for its prey can result in a difference between the body temperature of the predator and the prey thus being advantageous for the flying insect. Booster et al. (2015) hypothesized that at lower temperatures, the movement of the spider leg joints could be less coupled because of increased hemolymph viscosity thus slowing the flow of hemolymph, and demonstrated that at high temperature the spiders ran the fastest with the highest stride

frequencies using *Aphonopelma hentzi* (Jean-Étienne Girard) (Araneae: Theraphosidae) as model species.

The hunting behavior of a crab spider such as *S. globosum* consists of standing still with the first and second pair of legs (raptorial forelimbs) extended while waiting for a prey. When a prey approximates enough, the spider rapidly grabs it and brings it close to the mouthparts to be bitten. The effect of temperature on the hemolymph viscosity may improve the ability of *S. globosum* to catch a fly by increasing the attack movement velocity at higher temperatures. However, Schmalhofer and Casey (1999) found that temperature did not affect the hunting performance of the crab spiders *Misumenops asperatus* (Hentz) (Araneae: Thomisidae) and *Misumenoides formosipes* (Walckenaer) (Araneae: Thomisidae) on *Musca domestica* (L.) (Diptera: Muscidae). On the contrary, they reported a slight effect of temperature on the amount of time spent moving by the flies. Also, the prey were exposed to predators at set densities and within confined arenas, so that effect of encounter rate was irrelevant. As explained by Kruse et al. (2008), predator hunting success depends on the encounter rate with prey, prey escape ability, and predator agility; they also found that the predation rate of *Pardosa prativaga* (L. Koch) (Araneae: Lycosidae) and *Clubiona phragmitis* (L. Koch) (Araneae: Clubionidae) increased with temperature, their prey *D. melanogaster* being more active at the highest temperatures. This positive relationship between predation rate and prey activity on an increasing gradient of temperature can also explain our results for the significant increase of the maximum attack rate of *S. globosum* on *C. capitata* from 21 °C to 27 °C.

The two spider species we used to study the effect of temperature on the functional response use a sit-and-wait strategy to hunt. Overall, their attack rate and handling time were not significantly different across the studied temperatures. However, the handling time of *S. globosum* was significantly reduced from 21 °C to 27 °C suggesting a pattern that was then clearly uncovered by our method when we focused on the maximum attack rates. This highlights the relevance of the former parameter on studies related to biological pest control. Hence, differences in the functional response of these species resulted in an opposite pattern in the efficiency as predators against *C. capitata* along a gradient of temperature. Moreover, populations and food-web dynamics may depend on slight differences in functional response parameters (Vucic-Pestic et al., 2010) which may have important implications, for instance, in a climate change scenario.

5. Conclusions

In this work we showed how to obtain reliable and accurate simulated data and draw conclusions through simulation starting from low-effort laboratory trials (in our case only four samples and one replicate per spider species) within the context of functional response analysis. This enables a fast and direct comparison between the efficiency of different species of natural enemies in terms of the maximum attack rate under different conditions. Accordingly, research on functional responses under different environmental conditions and for different species of predators, parasitoids and their prey is crucial to increase the efficiency of biological pest control programs. In the case of spiders, known variables affecting pest suppression, such as mechanical silk properties, web architecture, humidity, body and environmental temperature, encounter rate, and prey behavior, need to be better investigated to determine their effects upon capture rate. We provided the **simaR** library in the highly extensible and Open Source R language that automates each step of a simulated functional response experiment based on real data. Using a bootstrapping process, the pest suppression potential of predators can be easily compared between potential natural enemies starting from low effort laboratory trials. This method could represent a powerful tool for using in the sustainable farming system context. However, it is not limited to pest control studies. In fact, it can be used to develop basic research on the biology of species and apply it to study the effects of climatic change on population dynamics and also

to provide valuable data for powerful individual based models (IMBs) that are of increasing interest nowadays such as ALMASS (Topping et al., 2003) and (Bilbao-Castro et al., 2015).

Authors' contributions

J.B.M., S.A.P.S. and J.A.P. conceived and designed the functional response experiments, J.B.M. developed the R functions, D.B. collected the spiders in the field and provided assistance during the laboratory experiments, J.P.S. reviewed and tested the code and all the authors contributed to writing the paper.

Data accessibility

The empirical functional response datasets used to test the code (Synema_dataset.txt and Araniella_dataset.txt), the **simaR** library (simaR_v05.R) and an example R file for type-II and type-III functional responses (Example_simaR.R) are available from <https://github.com/jbenma/simaR/tree/Simulation-functions>.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocontrol.2018.05.007>.

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