

Revisiting the influence of learning in predator functional response, how it can lead to shapes different from type III.

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Abstract

1. Predator/Parasitoid functional response is one of the main tools used to study predation behaviour, and in assessing the potential of biological control candidates. It is generally accepted that predator learning in prey searching and manipulation can produce the appearance of a type III functional response. Holling proposed that in the presence of alternative prey, at some point the predator would shift the preferred prey, leading to the appearance of a sigmoid function that characterized that functional response. This is supported by the analogy between enzyme kinetics and functional response that Holling used as the basis for developing this theory. However, after several decades, sigmoidal functional responses appear in the absence of alternative prey in most of the biological taxa studied.
2. Here, we propose modelling the effect of learning on the functional response by using the explicit incorporation of learning curves in the parameters of the Holling functional response, the attack rate (a), and the manipulation time (h). We then study how the variation in the parameters of the learning curves causes variations in the shape of the functional response curve.
3. We found that the functional response product of learning can be either type I, II or III, depending on what parameters act on the organism, and how much it can learn throughout the length of the study. Therefore, the presence of other types of curves should not be automatically associated with the absence of learning.
4. These results are important from an ecological point of view because when type III functional response is associated with learning, it is generally accepted that it can operate as a stabilizing factor in population dynamics. Our results, to the contrary, suggest that depending on how it acts, it may even be destabilizing by generating the appearance of functional responses close to type I.

Tweetable Abstract

In population dynamics, the association between learning and sigmoid functional response produces stability in predator-prey dynamics. Prey switching is the most accepted cause but is incompatible with experimental data. Using a model with a power-law learning curve, we found that learning also produces functional response curves which lead to instability.

46 **Keywords:** Power-law learning, Biological Control, Feeding Interaction, Functional Response Shape,
47 Predator-Prey, Prior Experiences.

48 Introduction

49 Most biological systems involve an array of intricate relationships among organisms which are of
50 paramount importance to understand the patterns of stability and biodiversity of communities
51 (McCann, 2000). Therefore, it is crucial to count on reliable methods to have the best predictions and
52 understanding of population and community dynamics, and eventually, to support wildlife
53 management decisions (Pettorelli et al., 2015).

54 Functional response (Holling, 1959; Solomon, 1949) is a mathematical framework used to
55 describe the ability of organisms to consume resources based on their availability. In this contribution,
56 we will refer to carnivores, herbivores, parasites, parasitoids, hyperparasitoids and some herbivores
57 that consume the whole plant (such as phytophagous plankton that eat algae) as “predators”. The term
58 “prey” here includes all different types of living organisms or food resources being consumed by the
59 predator. As the survival of predators depends on their ability to exploit variable densities of prey,
60 these organisms must be able to detect, process, and assimilate the prey as a function of its abundance;
61 this ability is influenced by several factors. According to Holling (1966), the three basic components
62 of the response of predators are *i*) the attack rate (linked to the ability to find prey: a); *ii*) the time prey
63 is exposed: t ; and *iii*) the handling time (how fast a prey is consumed: h). In a classical paper, Holling
64 (1959) characterized three types of functional response: type I response, in which the predator
65 consumes its prey at a constant rate regardless of the prey density, and therefore it results in a linear
66 relationship between prey density and consumption rate; the handling time is zero or near zero. Type
67 II response (Holling’s disc equation), in which saturation occurs mostly because the handling time
68 imposes a limit to the rate at which the prey is consumed, therefore it results in a rectangular
69 hyperbola in which the rate of prey consumed asymptotically approaches $1/\text{handling time}$. Finally, a
70 type III response is a sigmoidal curve. The mathematical reason for the change of shape is that
71 Holling’s disc equation now is a quadratic function of the prey density; the result is an “acceleration”
72 of the attack rate, but it keeps the limitation caused by handling time. The component that produces
73 this effect is learning (Holling, 1966). Real (1977) incorporated the possibility to shift between types
74 II and III functional responses by using the enzyme kinetic models of Barcroft and Hill (1910). In

Real's approach, the attack rate depends on a Power-Law of resource density as $a=bN^q$, where b is the attack coefficient, N is the number of preys in the environment, and q is an exponent that influences the shape of the functional response from a hyperbolic type II functional response ($q = 1$) to a strict type III functional response ($q = 2$) and beyond these bounds.

The population consequences of each type of response are different, for instance, the stability of predator and prey populations strongly depends on whether predator consumption rates increase linearly (type I functional response) or following a saturating function (type II and III functional responses) with prey densities (Hastings, 2013). Type III functional response is assumed to be able to stabilize predator-prey systems (C. Rall et al., 2008; Hassell, 1978; Hassell et al., 1977; Murdoch & Oaten, 1975) since its lower efficiency at low prey densities would allow the prey population to recover from population bottlenecks and, in consequence, avoid local extinctions. While at high densities, it would increase the speed of consumption, helping to avert outbreaking-type dynamics. However, the relationship between functional response types and stability is not simple. On the other hand, stability predictions differ depending on whether functional response parameters are derived. Several examples in predator-prey systems were recorded for a type III functional response, however, the influence of learning on attack rate and handling time, and the consequence of these changes on the functional response, are poorly known.

According to Holling (1966), type III curves (S-shaped) are indicative of organisms that show some form of learning behaviour. These organisms have developed general responsiveness to many stimuli and can filter out irrelevant stimuli. Likewise, they can learn and separately channel information from different stimuli. These channels are not permanently established since the learnt association will disappear unless it is reinforced or undergoes different experiences. The three key features of this behaviour are *associative learning*, *information channelling*, and *forgetting* (Holling, 1966). Such features give organisms great flexibility which allows them to focus on a few stimuli and still retain the ability to take advantage of changes in the environment. In dynamic populations, when the prey density is very low, the predator might not associate this stimulus with a reward because the prey is so rare. Conversely, if prey density increases, the predator could become more responsive to

the specific stimuli of the prey through learning. Tinbergen (1960) called this behaviour the development of a specific searching image.

Holling's model also reproduces prey switching, where the predator will consume preferentially (or more than proportionally), the most abundant prey. Thus, the predator will "switch" to another prey once the relative abundance of the different prey species reaches a critical threshold, which usually is near the inflexion point in the sigmoidal functional response curve. Based on the enzyme kinetics equation, the shape of the curve is mediated by an N parameter which is the number of encounters that a predator must have with its prey before the predator is maximally efficient in consuming that prey. As the N term multiplies, the curve becomes increasingly more like a switch function (Real, 1979).

However, many predators do not have access to alternative prey due to their specificity, like some biological control agents (Byeon et al., 2011), or under laboratory conditions, they are exposed to only one type of prey, however, they exhibit a type III functional response quite frequently (Dunn & Hovel, 2020; Van Lenteren et al., 2016; Yazdani & Keller, 2016). Consequently, a different type of learning should take place, not mediated by the presence of alternative prey, but by the accumulated experience of the organism when searching, manipulating and consuming prey. As in any learning process, the organism should then exhibit a learning curve (Shaw & Alley, 1985), in which the accumulated experience would translate into a modification of the functional response as a result of the experience.

Learning has been found extensively in almost all animal taxa (Manning & Dawkins, 1998; Shettleworth, 2001). These phenomena have long been described directly in parasitoid or predatory insects (Haverkamp & Smid, 2020; Little et al., 2019; Turlings et al., 1993; Vet et al., 1995). However, very few authors have studied how learning alters the parameters of the functional response curves, for example, Mendes et al. (2018), have found that, in egg predatory mites, the experienced females have significantly smaller manipulation times when compared to naive ones, but their attack rate is the same. Other authors investigated how pesticides affect predator efficiency, either because the predator attacks less prey or because of a decreasing searching time (He et al., 2012; Martinou & Stavrinides, 2015). These results show that learning can occur separately in attack rate or handling

time, which makes the enzyme kinetic approach not fully compatible with the results of laboratory experiments or monophagous insects. Therefore, to explore the relationship between learning and functional response, an alternative model is necessary.

In this study, we propose to explicitly incorporate learning curves in the parameters of the Holling's disk equation (functional response type II) and to analyze what changes are produced in the functional response shape by applied learning on its fundamental parameters, the attack rate, and the time of handling.

Methods

Model

As a starting point, we used Holling's disc equation of functional response type II:

$$dN/dt = aD / (1 + ahD)$$

where D is the prey density, a the attack rate, h the handling time, and N the consumed prey. The total consumed preys after a certain amount of time was called N_t .

A dynamic change based on the Power-Law of Practice (Snoddy, 1926) in a and h was added to the functional response type II model. So both parameters are allowed to change as a function of preys attacked, resulting in a monotonic increase and decrease of a and h , respectively as shown in Fig. 1.

For a , the model is a monotonically increasing Power-Law function expressed as an ordinary differential equation:

$$da/dt = -dN l_a (a_m - a)$$

$$\text{with } a > 0$$

$$\text{and } 0 < l_a < 1$$

where l_a is the learning rate of a per attacked prey, and a_m is the maximum possible attack rate for this species, with $0 < a_m < 1$. Here the attack rate a increases asymptotically from the initial a at the beginning of the experiment (a_0) to a_m at a rate of l_a . If $l_a = 0$, so there is no learning, but if $l_a = 1$, the learning is maximum, and a_m is approached after a single prey is consumed. How much it is possible to learn is $\Delta a = a_m - a_0$.

A similar Power-Law model was proposed for the handling time h , with the difference that in the case of h , it decreases with experience and asymptotically tends to zero instead of one as in the case of a , so

$$dh/dt = -dN l_h (h - h_m)$$

$$\text{with } h_m \rightarrow 0$$

$$\text{and } h \rightarrow 0.$$

where l_h is the learning rate of h per attacked prey, and h_m is the minimum handling time for this species. The handling time h tends asymptotically from h_0 (the handling time of the inexperienced predator) to h_m at a rate of l_h . How much it is possible to learn is $\Delta_h = h_0 - h_m$. Both Δ (Δ_a , Δ_h) are called *learning amplitude*.

Finally, if l_a , l_h , Δ_a , or Δ_h are equal to zero there is no learning and the functional response function becomes Holling's type II disk equation. The resulting dynamic of this model is shown in Fig. 1, both a and h depend on the initial condition (a_0 , h_0), the asymptotic values (a_m , h_m), the learning rate (l_a , l_h) and how much the predator can learn (Δ_a , Δ_h).

Prey depletion

The effect of prey depletion was also tested using the Rogers (1972) approach, in which the preys are a fixed pool in the experimental arena and are removed without reposiotion, so the differential equation is modified as:

$$dN/dt = aN_a / (1 + ahN_a)$$

$$\text{and}$$

$$dN_a = -dN$$

where N_a is the available prey, N_0 is the initial number of prey available, and N is the consumed prey, so $N = N_0 - N_a$. As a consequence, the available prey N_a is constantly removed and decreases asymptotically towards zero.

Analysis

Under a learning context, the function would be expected to be convex at low prey densities, because the improvement in the predator's ability to consume prey as a result of its experience is greater than its limitation in the ability to consume prey at a handling time greater than zero. At the inflexion point, the improvement in the ability of the predator to consume prey as a result of learning is exactly compensated at that point by the limitation in the ability to consume prey, so the function becomes purely limited by the manipulation time.

Therefore, a characteristic that allows identifying the type III functional response is its sigmoid convex-to-concave shape. There the function of consumed preys (N_t) as a function of density (N) such as in any sigmoid function has an inflexion point, so it is the second derivative zero. Before the inflexion point, the function is convex (positive second derivative), and after this point, it is concave (negative second derivative). In type II functional response, the second derivative is always negative and asymptotically approaches zero, and on type I response, it is always zero, as it is a linear function (Fig. 2). Therefore, the shape of the functional response was defined as the function of the second derivative of the functional response as a function of the offered preys. As explained above, the cases in which there was an inflexion point in which the second derivative was zero while decreasing from positive to negative values were classified as type III, if it was always negative, they were classified as type II, and if it was zero or near-zero, as type I. Additionally, if the slope of the second derivative was too low (near-zero), and it was barely noticeable, they were considered *near-type II*, and if the slope was low and always near zero, they were considered *near-type I*. The three functional response functions with their corresponding first and second derivatives are shown in Fig. 2.

To test whether learning in terms of improvement of attack rate and manipulation times generates type III functional responses, the analysis was aimed at identifying the different shapes of the functional response curve in different conditions of learning, here identified as parameters l_a and l_h . Other parameters affecting the behaviour of the functional response curve were a_0 , a_m , h_0 , h_m . To simplify the analysis, we assumed that $a_m = 1$ and $h_0 = 1$, so there are only four parameters to analyse, l_a , a_0 , l_h , and h_m .

To avoid the *curse of dimensionality*, the parameters were tested in pairs, with the ones influencing the attack rate being analysed separately from those influencing manipulation time. So one analysis was performed manipulating a_0 and l_a , and another with h_m and l_h . The tests were simulations at 1,002,001 combinations of parameters (a 1001 x 1001 matrix). For the attack rate a , the values used in the simulations were a range of a_0 between 0.01 and 1.0 at intervals of 0.01, and with a range of l_a between 0 (no learning) and 1 (maximum learning) at intervals also of 0.01. For the manipulation time h , the range of h_m values was between 0.1 and 0 at intervals of 0.01, always starting from 1, and a range of learning rates l_h as in l_a , with a range between 0 and 1, also at intervals of 0.01. All the analyses were performed without and with prey limitation (Holling, and Rogers models respectively).

Results

Learning attack rate

The simulations showed that under learning that improves attack rates, the functional response was predominantly of type II, especially at low rates of learning (Fig. 3), and at high levels of a_0 (initial attack rate). On the other hand, at low levels of a_0 , the response began to transition from type II to type III responses, as the learning rate increased.

In an intermediate zone, the functional response was characterized as near-type II, this response has characteristics of a type III response, such as a positive second derivative or close to zero, but very attenuated, so it is visually indistinguishable from a type II (Fig. 4).

At low initial attack rates (less than 0.3) and learning rates greater than 0.1, the functional response is a Holling type III. Interestingly, when the learning rate becomes very high (greater than 0.5), the near type II functional response again requires lower values of a_0 , since its inflexion point becomes very close to zero in very low prey densities, so the curve becomes closer to a type II at similar values of a_0 , but with lower learning values.

Under the Rogers model with prey depletion, the results are similar to those with constant density, the major difference is that the area in the parameter space in which the functional response is

type III and/or close to II, is slightly larger, reflecting the effect of the reduction in the number of preys available in the shape of the functional response. On the other hand, the maximum second derivative under the Rogers model is lower than with the absence of prey limitation.

Learning handling time

Simulations carried out with manipulation time learning showed results where most of the combinations of parameters produce type II functional responses. Only in combinations of parameters with very high learning rates and very low minimum manipulation times the functional response begins to differ from type II to resemble a type I (Figs. 5-6), within the upper left corner of the said graph ($l_h = 1$, and $h_m = 0$), the functional response is a type I.

As shown in Fig. 6, the learning of the manipulation time never generated visually similar functional responses to type III; on the contrary, as the learning rate l_h improved, the functional response looked more and more like a type I. When the minimum handling time (h_m) was very short, the curve equalled a type I, otherwise, the curve resembled an intermediate between a truncated type I and a type II. At low prey densities, the second derivative is always negative, only with very high learning rates ($l_h > 0.5$), the second derivative becomes slightly positive at higher prey densities, to become slightly negative again. This does not conform to a type III functional response, but rather a near-type I, because the derivative is very small, and the two critical points are unnoticeable. The effect of prey depletion was again small, with an area of type I functional response smaller than with Holling's model.

Discussion

Learning can produce all types of functional responses, depending on what parameters it affects. Under conditions of high learning amplitude, the functional response differed from type II. At low learning rates in both a and h , the result is a type II functional response, at high levels of learning in a prey-predator is type III, while at high learning rates in h , the resulting functional response approaches type I, so if $h_m = 0$, as the experiences accumulate, the handling time approaches asymptotically to

zero, and the functional response approaches $dn/dt = aN$, which is the functional response type I.

Learning can only produce type III functional responses if it affects the attack rate.

Theoretically, a linear functional response is possible when a predator can search and handle different prey simultaneously, or when the handling time is negligibly small (Hassell, 2000; Jeschke et al., 2002, 2004). A consequence of this work is that the type I functional response, which is usually interpreted as typical of filter feeders (Jeschke et al., 2004), or in general is not associated with learning processes, can be also a result of complex behaviours. Examples of type I functional responses have also been found in some parasitoid species (Kaçar et al., 2017; Mills & Lacan, 2004), and in filter-feeding birds (Arzel et al., 2007), a taxon of animals capable of learning complex behaviours. Arzel et al. (2007) found a switch point between two types I functional responses with different slopes, showing that the complexity of the foraging behaviour might imply several tasks that once optimized cannot be improved further and results in a curve with a series of discontinuities. Here we propose that this type of functional response is also a product of learning like type III, only that it is a different type since it has the same shape, but is caused by a different mechanism. So, it can be called type I_l if it is generated by learning, and type I_f if it is generated by filter feeding. On the other hand, learning in terms of improvement in the attack rate would produce responses increasingly similar to III, while if the learning occurs in the optimization of handling times, a type I_l response would be generated.

Prey depletion did not change the overall pattern of the results. The main difference is that the maximum second derivative under the Rogers model is lower than with the absence of prey limitation, reflecting that as the available preys are reduced with time, so do the opportunities to learn, as a consequence the second derivative is smaller. Therefore, in an arena with a limited number of preys, the animals learn less, because they run out of preys. Here, the appearance of a turning point is earlier due to depletion of the prey and not due to learning. So, the functional response is more often type III, but not because of learning. The effect of handling time was similar with an area in which the functional response is a type I or near-type I, smaller than without prey depletion. The main reason is that as the number of available preys decreases with time, the functional response begins to be limited

earlier, and keeps its functional response II shape even though its handling time decreases to a near-zero value.

In terms of population dynamics, it is generally accepted that the type III functional response may have stabilizing effects on prey dynamics as proposed by Oaten and Murdoch (1975), the reason is the increase in the probability for a prey to be killed as their density increases, which means the presence of a positive second derivative on the functional response curve, as in the type III curve. Here we observed that this phenomenon (the transition from a type II response to a type III) occurs only in the case of strong learning in attack rate, but not in learning in handling time. However, the handling time learning produces a curve with an asymptote that increases with time and prey density, which can give a different type of stabilization that requires further more specific studies.

Another issue is that, since learning is an accumulated process, it will interact with population dynamics in the form of a delayed effectiveness response. For example, given that the prey population will decrease after a peak or outbreak as some herbivorous insects as described by Berryman et al. (1987). Under the approach used here, with cumulative learning, some predators might remain more effective for a while after a decrease in prey population. In the case of parasitoids, as the lifespan is the same as its hosts it is not an issue, while in the case of vertebrate insectivores it will cause further instability or local extinctions, by consuming more than proportionally when the population is small after an outbreak.

Conclusions

The results obtained in this study show that learning can change the functional response of predators in different ways since it is generally accepted in the literature by generating either type I, II or III and intermediate forms in the absence of alternative prey. Therefore, learning can both be a stabilising or destabilising factor in the population dynamics, depending on which type of prey consuming behaviour it affects.

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315 **Authors' Contributions**

316 B.O.A supervised the project. All authors conceived the ideas and designed the methodology. B.O.A
317 designed the mathematical models and conducted the analysis. All authors contributed to writing and
318 revising the manuscript and gave final approval for publication.

319 **Conflict of interest statement**

320 The authors declare no competing interests.

321 **Data accessibility statement**

322 The manuscript does not use any data.

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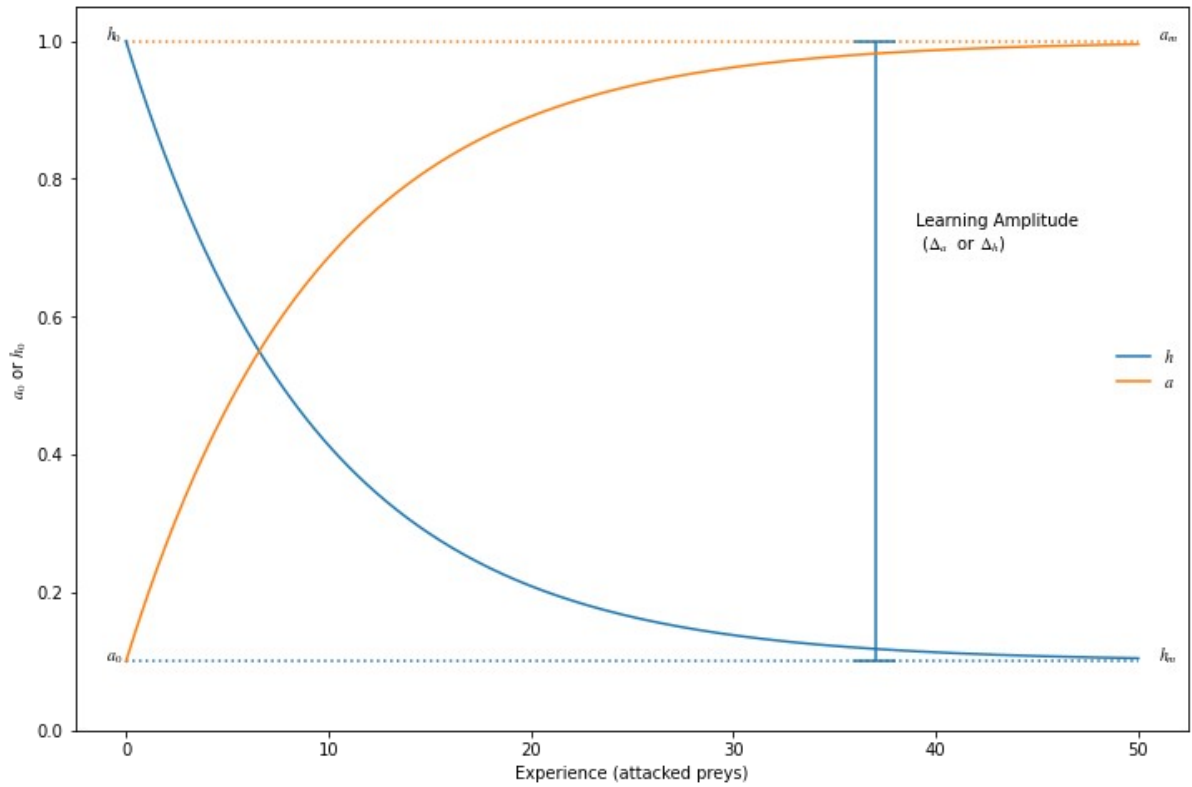
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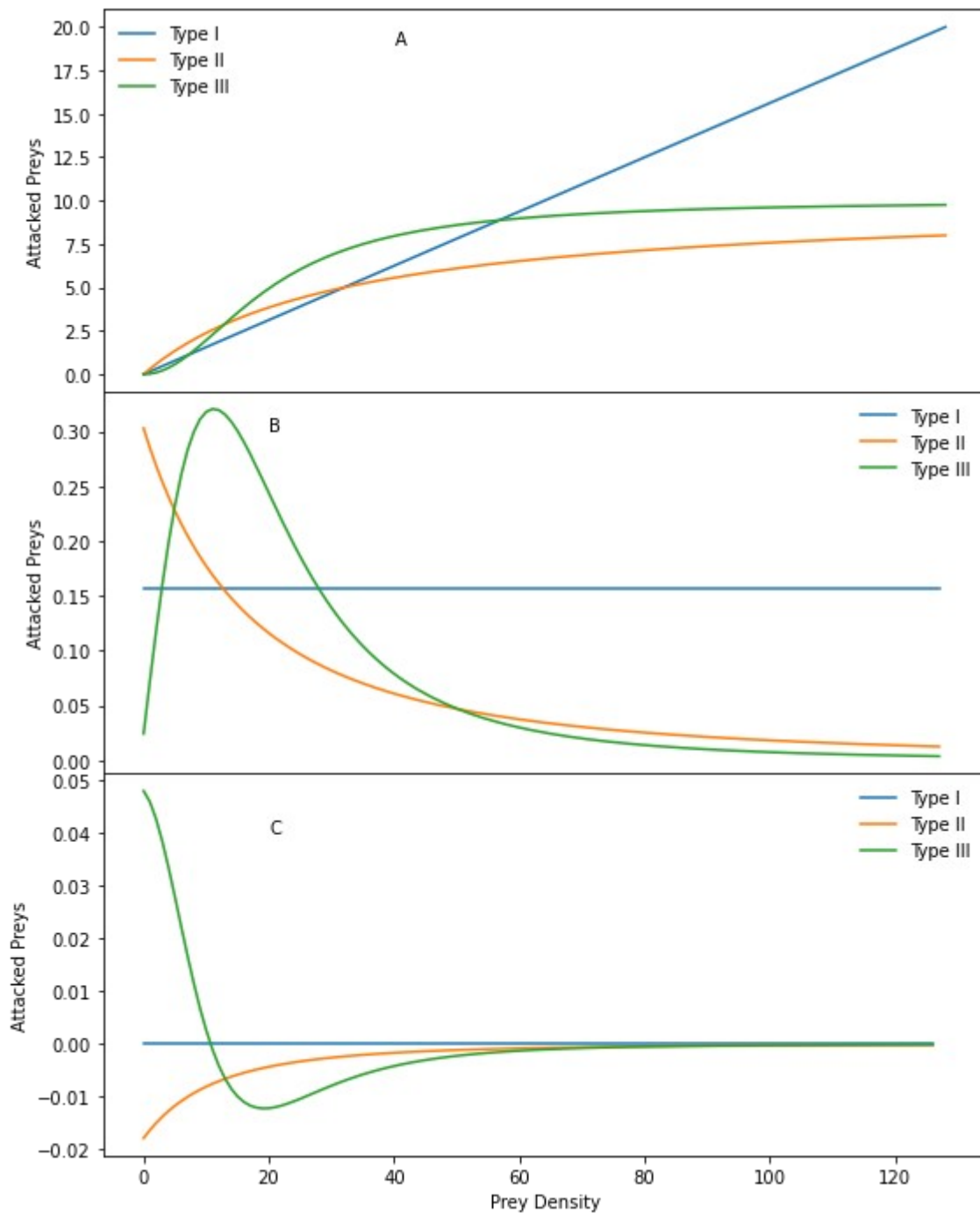
423 Figures

424 **Figure 1**



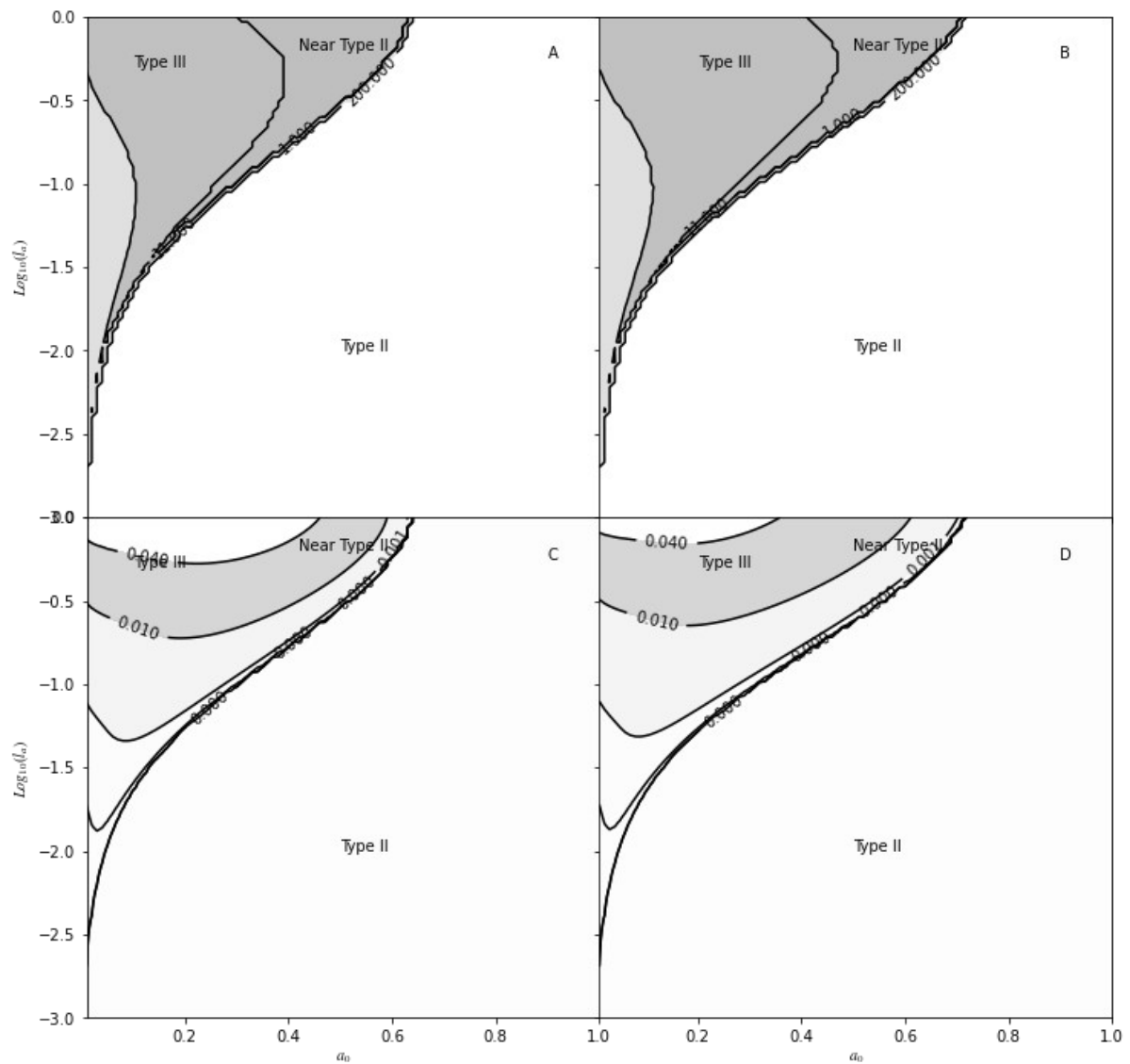
425 Learning curves proposed for the handling time (h) and the attack rate (a), both curves are of the
 426 Power-Law type, where they tend exponentially to a final asymptotic value from an initial point. h_0
 427 and a_0 are respectively the initial values of the handling times and the attack rate, while h_m and a_m are
 428 the final values of both variables. The learning amplitudes (Δ_a , Δ_h) are defined by the distances
 429 between the initial and final values of h or a .

430 **Figure 2**



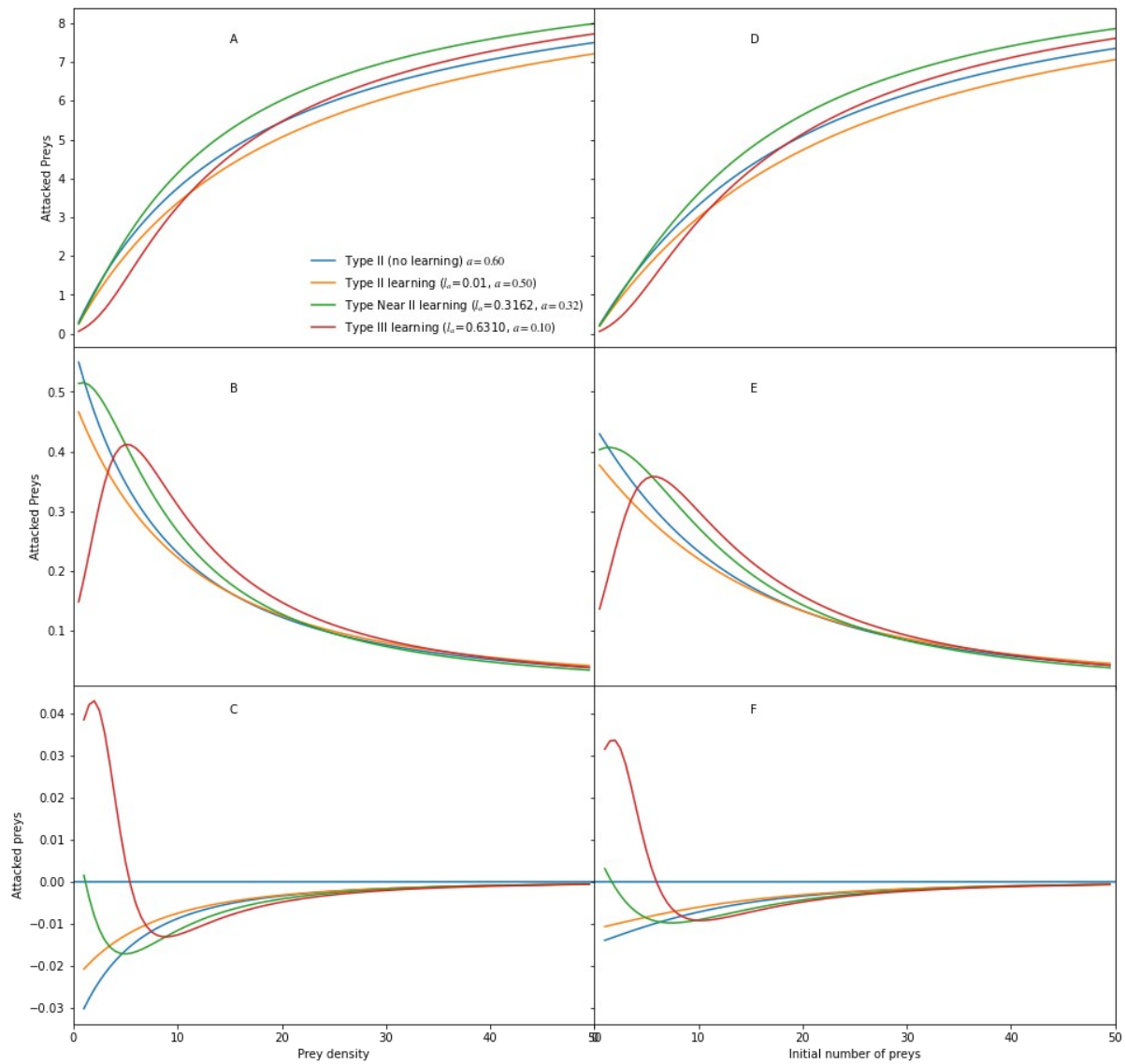
431 Preys attacked as a function of preys offered for Holling's three functional responses (A), B is the first
 432 derivative of the function, and below (C), the second derivative. The type III functional response can
 433 be characterized by the presence of an inflexion point in the slope of the curve, while the other two do
 434 not contain critical points of any kind.

435 **Figure 3**



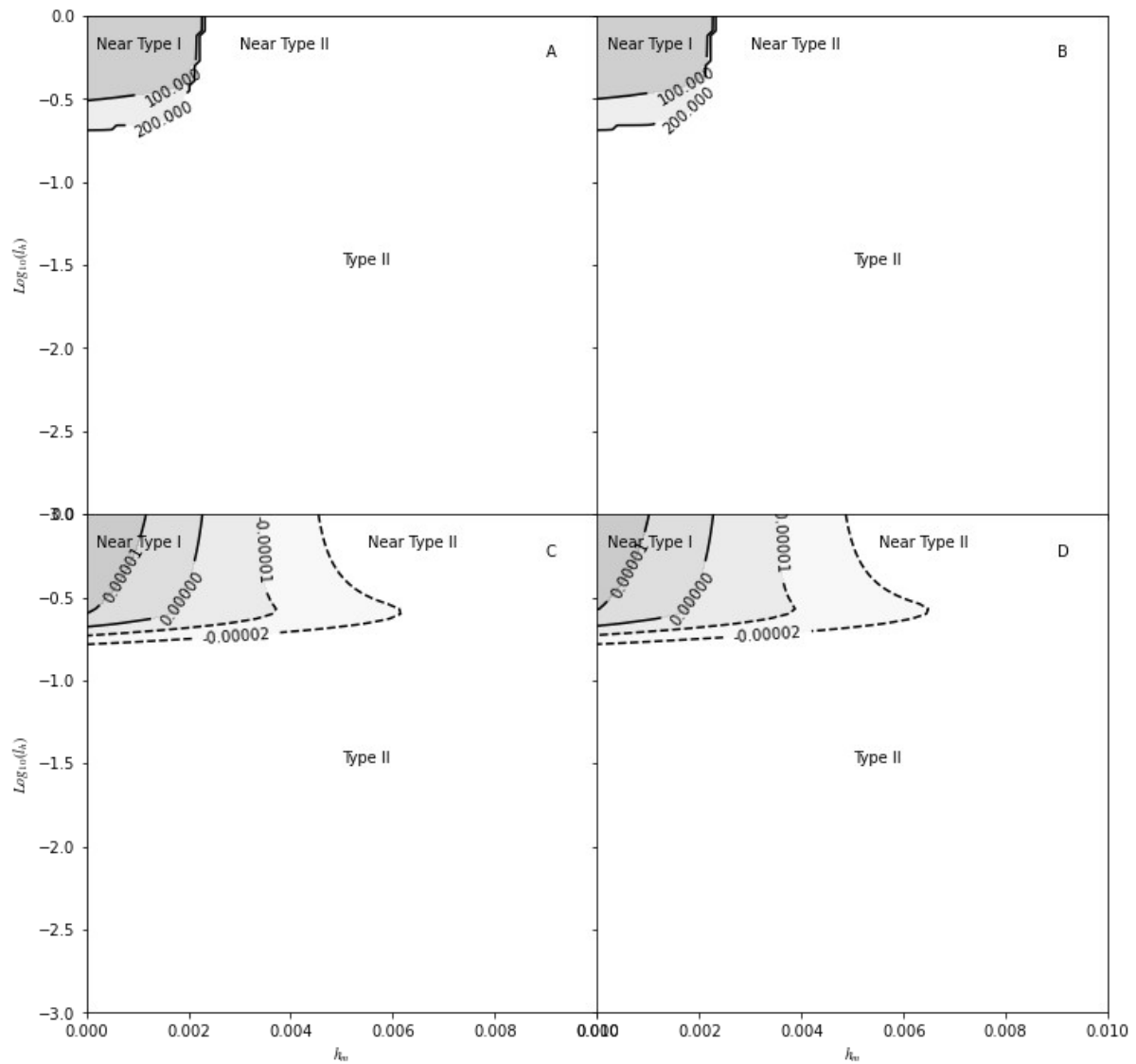
436 Functional response as a function of the combination between the logarithm of the learning rate (l_a) on
 437 the Y-axis, and the initial value of the attack rate (a_0) on the X-axis, without limitation by prey (A, C)
 438 and with limitation (B, D). In graphs A and B, the grayscales and contour lines show the prey density
 439 (N) at which the first inflexion occurs. Graphs C and D, on the other hand, show the maximum value
 440 of the second derivative of the functional response curve. Maximum values of second derivative
 441 greater than zero indicate type III functional responses, values close to zero, but positive, are near-
 442 type II functional responses, finally, negative values indicate type II functional responses.

443 **Figure 4**



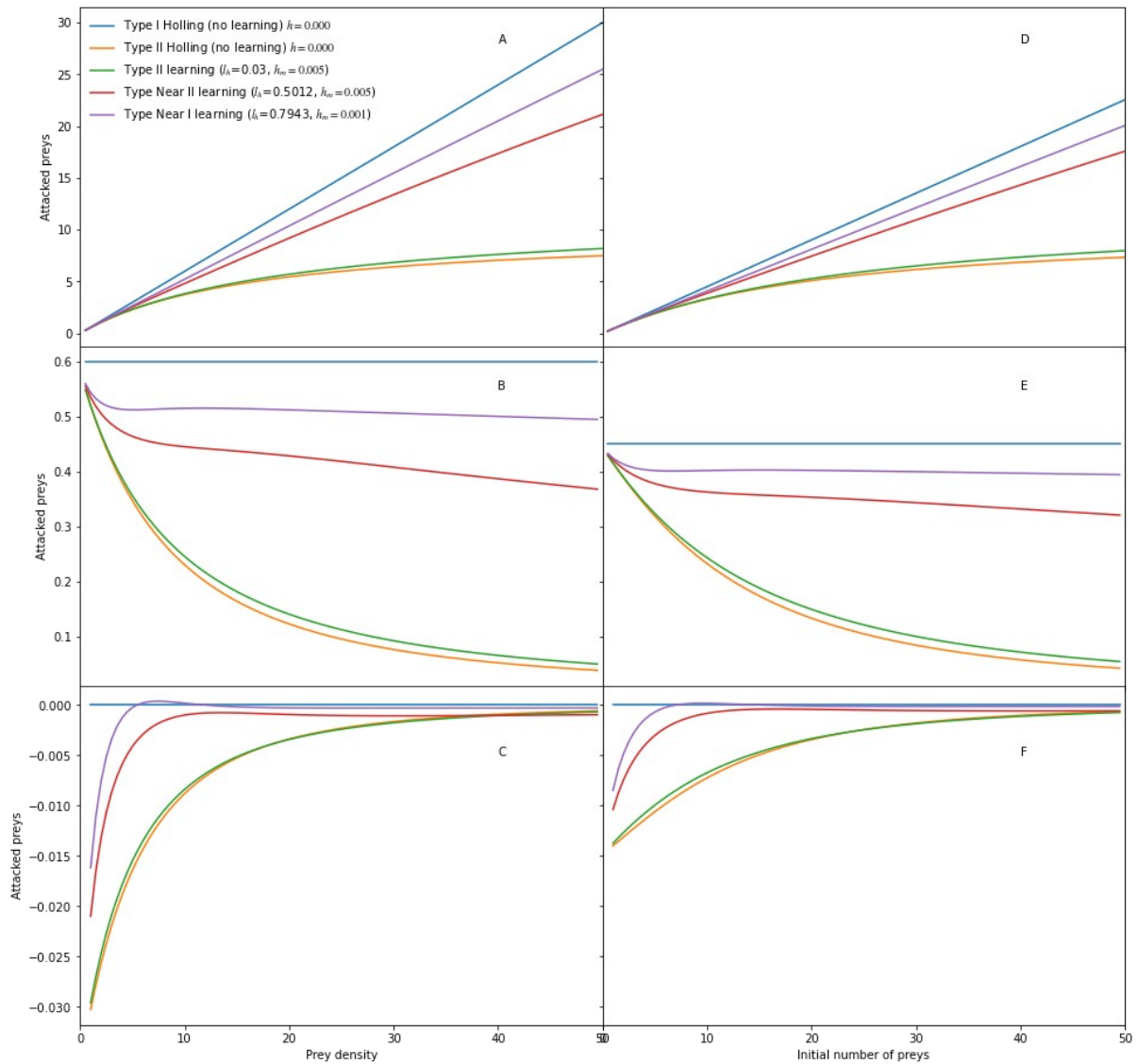
444 Consumed preys as a function of offered preys under different learning (l_a) rates for attack rate (A, D),
 445 and first (B, E) and second derivatives (C, F). Plots A, B, and C are the models without prey
 446 depletion, so the X-axis is the prey density, while D, E, and F are with depletion according to the
 447 Rogers model, therefore the X-axis is the initial number of prey. With high learning rates, the
 448 functional response approaches type III functional response (positive second derivative at low prey
 449 density as a consequence of learning, and then negative as a consequence of handling time limitation).

450 **Figure 5**



451 Functional response as a function of the combination between the logarithm of the learning rate (l_h) on
452 the Y-axis, and the minimum handling time (h_m) on the X-axis without prey depletion (A, C) and with
453 prey depletion (B, D). In graphs A and B, the grayscales and contour lines show the prey density (N)
454 at which the first inflexion point occurs. Graphs C and D, on the other hand, show the maximum value
455 of the second derivative of the functional response curve. Maximum second derivative values greater
456 than zero indicate type I functional responses, values close to zero, but negative, are near-type II
457 functional responses, finally, negative values indicate type II functional responses.

458 **Figure 6**



459 Consumed preys as a function of offered preys under different learning (l_h) rates for handling time (A,
 460 D), and first (B, E) and second derivatives (C, F). Plots A, B, and C are the models without prey
 461 depletion, so the X-axis is the prey density, while D, E, and F are with depletion according to the
 462 Rogers model, therefore the X-axis is the initial number of preys. With high learning rates, the
 463 functional response approaches type I functional response (positive second derivative at low prey
 464 density as a consequence of learning, and then negative as a consequence of handling time limitation).