Opportunistic random searcher versus intentional search image user

József Garay[1, 2], Zoltán Varga[3], Tamás F. Móri[4], Inmaculada López[5],
Manuel Gámez[5,6], Juan R. Gallego[6], Tomás Cabello[6]

[1]MTA-ELTE Theoretical Biology and Evolutionary Ecology Research Group and Department of Plant Systematics, Ecology and Theoretical Biology, Eötvös Loránd University, Pázmány Péter sétány1/c, H-1117 Budapest, Hungary. [2]MTA Centre for Ecological Research, Evolutionary Systems Research Group., Klebelsberg Kuno utca 3, Tihany 8237, Hungary. [3]Department of Mathematics, Szent István University, Páter K. u. 1.H-2103, Gödöllő, Hungary. [4]Department of Probability Theory and Statistics, L. Eötvös University, Pázmány Péter sétány1/c, H-1117 Budapest, Hungary. [5]Department of Mathematics, University of Almería. La Cañada de San Urbano 04120 Almería, Spain. [6]Center for Agribusiness Biotechnology Research, Almería University, Ctra. Sacramento s/n, ES-04120 Almería, Spain. Correspondence and requests for materials should be addressed to J.G. e-mail: garayj@caesar.elte.hu

Keywords: activity distribution, functional response, intentional forager, numerical response, optimal foraging, one predator – two prey system, traveling time.

Abstract

We consider two types of optimal foragers: random searcher and search image user. A search image user can find its desired prey with higher and the undesired prey with lower probability than a random searcher. Our model takes into account the density dependent traveling time and the time duration of reproduction (oviposition). In the framework of optimal foraging theory for one predator – two prey systems, we find that there are ranges of prey densities where the search image user, and there are other ranges of prey densities where the random searcher has higher net energy intake. Experimentally, we found that *Nabis* is a search image user in the above sense.

Introduction

In this paper we are interested in what the effect of the search image is on optimal foraging. We use the definition of search image by Dukas[1]: It is a "*selective search for a particular cryptic prey type, which involves an increased probability of detecting that prey type and a reduced probability of detecting other distinct prey types*". Observe that search image implies a trade-off between the encounter with preferred and non-preferred prey type. In our words: the *search image user* (**SIU**) can find its desired prey with higher probability and its undesired prey with lower probability than a random searcher. In the standard optimal foraging models, the forager is a *random searcher* (**RS**), i.e. its prey preference does not affect the encounter probability with prey types, in other words, encounter probability is only determined by preys' densities.

In predation, encounter is one of the most important steps[2,3]. Finding the prey is a complicated stochastic process[4] and the encounters are determined at least by two main factors: the perception ability of the predator[5] and the prey densities[6]. Here we will consider the case when the predator finds its desired prey with a high, density independent probability, but the travelling time[7] of the predator will be longer at lower prey density. In a one predator – two prey system the question arises: Either the **SIU** or the **RS** has higher net energy intake?

We note that in greenhouses these systems often occur. The prey preference of the agent is important in biological control. For instance, if the agent's preferred prey make less damage than the non-preferred prey, then the economic efficiency of the agent is not optimal[8,9]. The basic picture is motivated by the behaviour of certain predatory insects that practically forage continuously, except egg laying. (e.g. *Nabis pseudoferus* Remane displays such behaviour[10]. *Nabis* would eat all day long, hence the time of laying eggs reduces the time available for predation. The latter fact, in particular, will play an important role in the calculation of the numerical response.

Theoretical study

Assumptions In a habitat of area M, there are H perception ranges (PR-s), x is the number of A-prey, y the number of B-prey, and we suppose that $x + y < H$. Assume that the habitat is homogeneous[6,11], i.e. in all PR-s predator-prey interactions are the same. For an example, we can consider the following situation: A predator insect searches prey on a given plant, and the perception ranges are leaves.

For simplicity, we have assumed that the prey have no anti-predator behaviour, i.e. the predator can kill any encountered prey. In particular, both prey can neither self-defend against the predator nor flee[12], they do not have gregarious behaviour[13] and there is no refuge[14]. The above simplifying assumptions imply the prey has no effect on predation, so we will have an optimal foraging model where the predator maximizes its numerical response. Each perception range contains at most one prey, so prey types are randomly separated in the PR-s in the home range of the predator. There is a stationary distribution of perception range types PR:X (X=E (empty), A, B), which does not change during time T, say one day.

The optimal forager predator has territory, so there is no interaction between two predators during hunting[15,16,17]. For simplicity, we also assume that there is no nutritional difference between different prey types, except energy content[18]. The searching processes of the predator and the distribution of prey are independent. The traveling time to find a prey depends on the density of the prey, it is longer at lower prey density. A **RS** visits the nearest perception range and the random distributions of prey ensure the random encounters. A **SIU** uses a search image and finds its desired prey type with density independent probability. We will compare the numerical responses of two types of predators.

What is the numerical response, if the reproduction also needs time? In optimal foraging theory, a widely used assumption is that the numerical response equals the functional response weighed with a conversion coefficient. However, if the reproduction (oviposition or offspring care) also needs time (similarly to searching for prey and handling of prey), moreover, the reproduction and hunting exclude each other, then the numerical response and the functional response are not just proportional. We emphasize the assumption that the time durations of the predator's activities do not overlap, is one of the basic requirements for the derivation of functional responses[2,7].

For *Nabis*, during the time period T, the predator either predates (T_P denotes the total time duration of predation during T), or lays eggs (T_E is the total time duration of laying eggs during T), and the reproduction and the predation exclude each other, so we have $T = T_P + T_E$. The number of eggs, however, also depends on the collected energy, so T_P and T_E are not independent. Based on the energy balance for the time period T, in **SI.1** we calculate the numerical response

$$W(\mathbf{s}) = \frac{E(\mathbf{s}) - E_{CL}}{E(\mathbf{s})t_E + E_E},$$

where $E(\mathbf{s})$ is the energy intake in unit time by predator using a foraging strategy **s**, E_{CL} is the cost of living of a female predator in unit time, and E_E is the energy cost of one egg (also including the searching cost for a good place for the egg and the energy cost of egg laying), and t_E is the time duration of laying one egg, $t_E > 1$. Observe that the numerical response is a strictly increasing function of the energy intake in unit time of predation. In particular, the numerical response and the energy intake will take their maxima at the same foraging strategy.

Searching time and travelling time. Our basic assumption is that whatever the PR type the searching predator finds, it will be the nearest one from that type. Now searching time τ_S has two components: the first one is travelling time τ_{TX} (X=E,A,B), which depends on the density of A-prey and B-prey, the second one is local searching time τ_{LS} in the PR. For simplicity, we assume that τ_{LS}

does not depend on what the focal PR contains. So we have $\tau_S = \tau_{TX} + \tau_{LS}$. In **SI.2** we proved the following: If type PR:X has density λ_X, and is randomly distributed, then the average distance between the nearest PR:X and the predator is the following: In one dimension (for a predator moving along a straight line) it is $\frac{1}{2\lambda_X}$, in two dimensions (predator moving along in a plane) it is $\frac{1}{2\lambda_X^{1/2}}$, while in 3 dimensions it is approximately $0.55396\lambda_X^{-1/3}$. We emphasize that the dimension of the travelling mode of the predator has an important effect on the functional response.

Now we are in a position to calculate the optimal foraging strategy for the two types of predators.

Random searcher does not use search image. RS is similar to a forager in the standard optimal forging model[19]. However, we have two novel points: **RS** looks for the nearest PR, so its traveling time depends on the density of PR. Moreover, **RS**'s numerical response also depends on the oviposition time. As mentioned above, the numerical response will reach its maximum at the same strategy as the average energy intake, thus **RS** applies the well-known zero-one rule[19], namely

$$s_A^* = 1 \text{ and } s_B^* = \begin{cases} 0, \text{ if } x > \dfrac{\tau_S c_B}{c_A \tau_B - c_B \tau_A} H \\ 1, \text{ if } x < \dfrac{\tau_S c_B}{c_A \tau_B - c_B \tau_A} H \end{cases},$$

where c_A, c_B are the energy contents and τ_A, τ_B the handling times of A-prey and B-prey, respectively. (For mathematical details see **SI.3**). In the usual sense, we say that A is more valuable than B, if $\frac{c_A}{\tau_A} > \frac{c_B}{\tau_B}$. While the more valuable prey type is abundant, **RS** will only accept this type, ignoring the other one. If the more valuable prey type is rare enough, then it opportunistically accepts both prey types, see Figure 1.

Search image user. For simplicity, we assume that **SIU** can find its nearest desired prey with probability 1, so **SIU** cannot find an empty PR. **SIU** has two searching modes: when looking for an A-prey, it cannot encounter a B-prey, and vice versa. Thus this kind of predator has only one-dimensional optimal foraging strategy, it looks for an A-prey with probability *s*, and for B-prey with probability 1-*s*. Furthermore, there are two density dependent traveling times corresponding to the desired prey type: τ_{TA} and τ_{TB}. In **SI.4** we calculate the optimal foraging strategy and find that

$$s^* = 1, \text{ if } \frac{c_A}{t_A} > \frac{c_B}{t_B}; \text{ and } s^* = 0, \text{ if } \frac{c_A}{t_A} < \frac{c_B}{t_B},$$

where $t_A = \tau_{TA} + \tau_{LS} + \tau_A$ and $t_B = \tau_{TB} + \tau_{LS} + \tau_B$ are the density dependent time durations of a round of killing an A-prey and a B-prey, respectively. Thus **SIU** only accept the prey type that ensures higher energy intake rate during the whole time period *T*, see Figure 1.

We note that if **SIU** can find its nearest desired prey with probability less than but near enough to 1, then **SUI** can also be opportunistic in the sense that when looking for B-prey it finds an A-prey, then **SIU** may kill this A prey, as well. Observe that the trade-off of search image implies a trade-off between intentional and opportunist, since **SIU** has less chance to be opportunistic.

Does search image user overperform random searcher? First, in Figure 1 we demonstrate, that different types of predators have different optimal foraging strategies, i.e. their switching behaviours are different (mathematical details in **SI.5**).

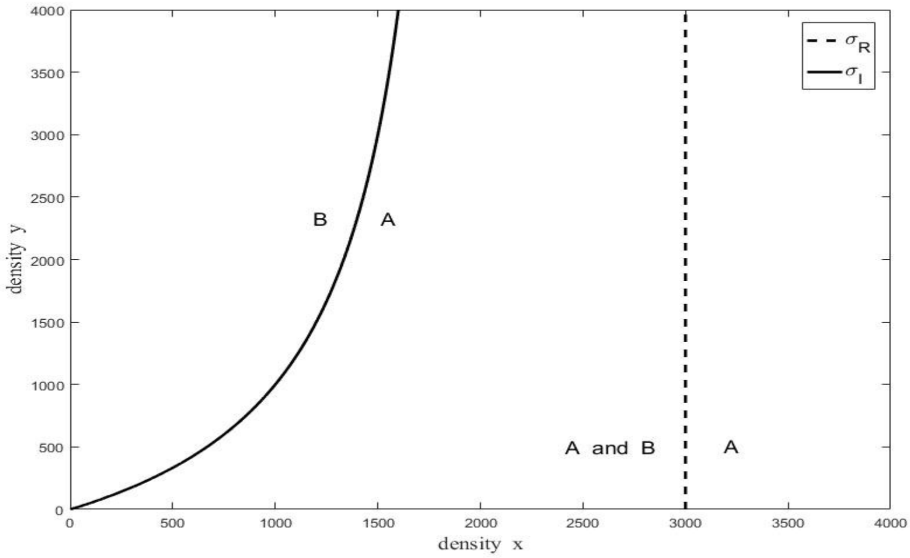

Figure 1. Switching curve σ_R separates density ranges where **RS** eats only A (right side) and eats A and B (left side). Switching curve σ_I separates density ranges where **SIU** searches A (right side) and searches B (left side).

Considering several rounds of predation, the sequences of encountered prey types for **RS** and **SIU** are different, since **RS** encounters randomly with both prey types, according to the prey densities; to the contrary, **SIU** encounters its preferred prey type with higher probability. Observe that in Figure 1, in the density range to the right from σ_R, both **SIU** and **RS** only consume the more valuable A-prey, thus killing sequences are the same, and in spite of that, their encounter sequences are different.

Now the question is: which type of predator has higher energy intake in unit time at fixed densities *x*, *y*? We found that there are two prey density ranges where **SIU** collects more energy than **RS** does. Intuitively, when A-prey is scarce and B-prey is abundant, then **SIU** kills more B-prey, and **RS** kills very few A-prey. Furthermore, if A-prey is abundant then both predator types accept only A-prey, but **SIU** kills more A-prey than **RS** does. Moreover, there is a range of prey densities where **RS** performs better in energy intake than **SIU** does, see Figures 2 and 3.

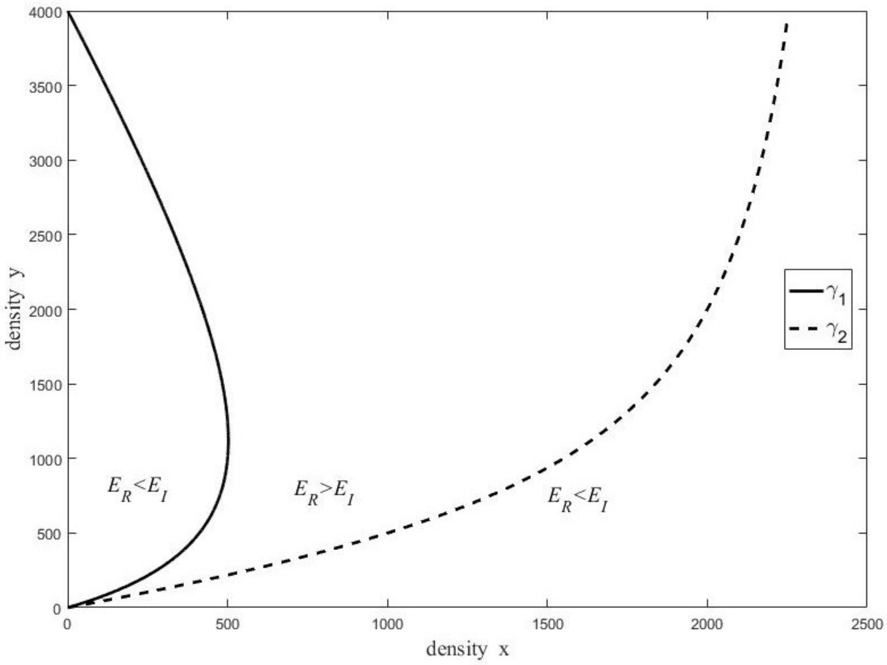

Figure 2. In the range between curves γ_1 and γ_2, **RS** collects more energy in unite time (E_R) then **SIU** (E_I). Curve σ_I of Figure 1 would split range $E_R>E_I$ into two parts.

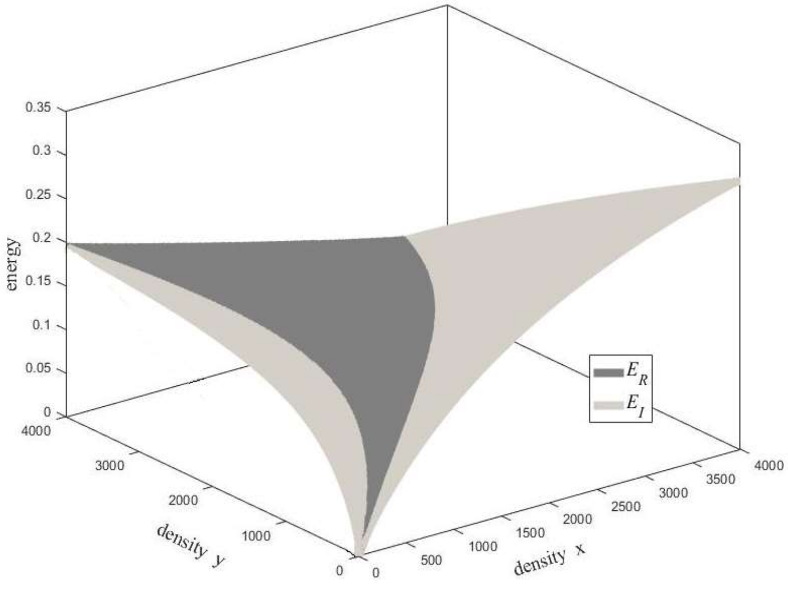

Figure 3. Upper hull of energy surfaces $E_R(x,y)$ and $E_I(x,y)$

The main intuitive reason for the latter is the opportunism of **RS**[2,13]: In the range where $E_R(x,y)>E_I(x,y)$, **SIU** kills only one type of prey, while **RS** opportunistically exploits both types of prey.

Now we are in the position to get some insight into our main question: Does **SIU** overperform **RS**? Not necessarily. We have two main cases:

First, assume that the population dynamics of the three-species system has a stable equilibrium. If the equilibrium prey densities lie in the range where **SIU** has higher energy intake, then **SIU** overperforms **RS**. If the equilibrium lies in the range where the **RS** has higher energy intake, then **RS** over performs the **SIU**.

Second, assume that the population dynamics of the three-species system has no stable equilibrium, but e.g. there is a cyclic coexistence where the cycle touches all types of prey density ranges. Then the optimal foraging strategy will be a mix: the predator uses either search image or random search according to the current prey type densities.

Experimental study. Results

We have shown indirectly that Nabis uses a search image. First we observe that *Nabis* is an opportunistic predator, i.e. if it encounters a prey, always kills it. So its killing sequence and its encounter sequence are the same. First, we checked the randomness of the encounter sequence of *Nabis*. In **SI.6** we introduced a new test for that, and found that *Nabis* encounter sequence is not random (P=0.009). The Manly preference index (α) supports these results. Thus, the value of α indicates preference when it exceeds 0.5, rejection when it is lower than 0.5 and indifference when it is exactly 0.5. In our trial, *Nabis* showed a clear preference for *S. exigua* larvae (heterospecific prey) ($\alpha_1 = 0.65 \pm 0.14$) and rejection of conspecific nymphs ($\alpha_2 = 0.35 \pm 0.14$) (Wilcoxon test $P = 0.009$).

Summary: Although *Nabis* has more complex behaviour than our theoretical model, we have found that cannibalistic *Nabis* uses search image, but not absolute intentionally, since it can encounter with not desired prey type too, but its encounter sequence is not determined by its preys' densities, i.e. it encounters its preferred prey with higher probability than its conspecific. This corroborates the results found on the subject and published elsewhere[20].

Discussion

Some insight into the use of search image may be useful from theoretical and applied ecological point of view. In theoretical ecology, one of the possible mechanisms to maintain diversity is the negative frequency-dependent selection, i.e. rare prey experience higher survival than a more common type. Search image formation has been invoked as a possible, proximate explanation[21].

Although we concentrate on *Nabis*, our theoretical model gives some general insight. Firstly, since the numerical response takes its maximum at the maximum of energy intake, our results are also valid for the case when the reproduction time constraint has no effect on the foraging process. Thus, our result that **SIU** does not necessarily collect more food than **RS,** is valid in general. Consequently, our hypothesis that optimal forger must use mixed behaviour: either is intentional search image user or opportunistic random searcher (but only one at a time), according to the density of its prey, should be tested.

Another possibility is, if **SIU** is not purely intentional (i.e. if it reaches its preferred prey type with probability less than one). As we found, *Nabis* falls into this category, since its encounter sequence is not randomly determined by prey density. In this case opportunism is also possible.

For an outlook we note the mechanism of our theoretical model may be also applied in the context of other situations of food choice, also relevant for the biological control of pests, carried out with a significant number of predatory species[22,23,24]. Following[25], they may be classified according to their diet or by their role in ecological food webs, in "predators" and "true omnivores". In turn, the former may be specialist and generalist predatory species[26]. Generalist arthropod predators typically are bitrophic: they simultaneously occupy the third and fourth trophic levels by virtue of feeding both on herbivores and on each other. Moreover, most generalist predators are cannibals[27]. In turn, true omnivorous arthropods feed on both herbivores and plants[23].

According to the above, the results found in the present work and in relation to the biological control can be considered in a one predator - two prey system in two situations: (i) one omnivorous predator - two prey, (ii) generalist predator that presents cannibalism; in this situation it would be one generalist predator - two prey (conspecific and heterospecific prey).

The first assumption can be represented by two events. The true omnivorous *Nesidicoris tenuis* (Reuter) (Hemipera, Miridae) and their prey *Bemisia* tabaci (Gennadius) (Hemiptera, Aleyrodidae) and *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) in greenhouse tomato crops, when both pest species are present in the crop there is a poor biological control of the second one[28]. Another example is represented by the true omnivorous *Macrolophus pygmaeus* (Rambur) (Hemipera, Miridae) in the same conditions and pest species[29,30]. In the second case, generalist predator with cannibalism, can be represented by the species studied here in the experimental part: *N. pseudoferus*. In this case it has been demonstrated that in the presence of conspecific, adult females use **SIU**. This results in a less efficient biological control of the pest species[20]; as it has been demonstrated in other studies[31]. There are similar results in relation to cannibalism in the case of the general predator mite *Typhlodromus pyri* Schueten (Acari: Phytoseiidae) agents against tetranychid pest mites of apple[32]. All the above quotations can only be explained, if omnivorous uses **SIU** instead of **RS**.

The main property of the search image[1] is that prey preference of forager does affect the encounter probability of its prey types. Thus, if an encounter sequence is known, applying the methodology proposed by us, one has the possibility to check whether the predator uses search image or not.

In summary, SIU versus RS seems to be one of the crucial factors that should be considered if omnivorous and generalist species are used for biological control in agricultural ecosystems. Especially, as mentioned above, according to the current trend of biological control that consists in the use of predatory species generalist and, more vigorously, in the case of omnivorous species.

Method

In *theoretical part* we use mathematical tools.

Experimental trial: The trial methodology was adapted from[10,20]. *N. pseudoferus* adult mated females were used less than one week after final nymphal ecdysis. They were individually isolated in Petri dishes and subjected to a starving period of 24 h prior to testing. They were only given a piece of sponge moistened with distilled water. Six specimens of second-instar larvae of *S. exigua* as heterospecific prey and six specimens of second-instar nymphs of *N. pseudoferus* as conspecific prey, were introduced in a choice arena (Petri dish); then an only *N. pseudoferus* adult female was also introduced. Each adult female predator was left to prey on them for a period of 4 h. Fifteen replicates were carried out for each treatment. Two types of data were recorded: a) the number of prey killed was annotated at the end of the trial (4 h), and b) the prey-capture sequence by adult females was also recorded. Since direct human observation may interfere with the predation behaviour of *Nabis* species[33], we photographed the trial arena every 10 seconds using an Eos 550D (Canon®) digital camera, EFS 18-55 lens with macro function (Canon®), connected with a cable to a computer. The software used was Communication Software for the Camera EOS Utility, version 2.14[34]. Photographs were set in time-lapse using the Image Processing and Analysis in Java (ImageJ) software, version 1.49[35], which recorded the identity of the killed prey, and the sequence of predation events. Adult predators' preferences towards different offered prey was studied using the Manly preference index (α)[36]. As established by Cock[37], the Manly index is the only method that takes into account the reduction in prey density that occurs during the course of the trial. This has been corroborated in the review by Sherratt and Harvey[38]. The index equation is as follows:

$$\alpha_i = \frac{\frac{r_i}{N_i}}{\frac{r_i}{N_i} + \frac{r_j}{N_j}}$$

where r_i = number of prey i consumed, r_j = number of prey j consumed, N_i = number of prey i offered, and N_j = number of prey j offered. Comparisons of preference indexes were carried out using the Wilcoxon signed-rank test.

Acknowledgement. This work was partially supported by the Hungarian Scientific Research Fund GINOP 2.3.2-15-2016-00057 (to J.G.).

Author Contributions statement: JG, ZV and TC designed the study; TFM calculated the nearest prey in different dimension, JG, ZV and MG analysed the theoretical model; MG calculated the numerical examples and made the figures, TFM and IL made the new randomness test in the encounter sequence of Nabis, TC designed and directed the experiment on Nabis, JRG carried out the trials, TC calculated the preference index for Nabis, JG, ZV, TFM and TC collaborated in writing the article.

Competing Financial Interests: None.

References

1. Dukas, R. Behavioural and ecological consequences of limited attention. *Phil. Trans. R. Soc. Lond. B* **357**, 1539–1547 (2002).

2. Garay, J. & Móri, F.T. When is the opportunism remunerative? *Community Ecol.* **11**, 160-170 (2010).

3. Cressman R, Křivan V, Brown J. S. & Garay, J Game-Theoretic Methods for Functional Response and Optimal Foraging Behavior. *PLoS ONE* **9(2)**: e88773 (2014).

4. Humphries, N.E. & Sims, D.W. Optimal foraging strategies: Lévy walks balance searching and patch exploitation under a very broad range of conditions. *J. Theor. Biol*. **358**, 179-193 (2014).

5. Pietrewicz, A.T. & Kamil, A.C. Search Image Formation in the Blue Jay (Cyanocitta cristata). *Science*, **204**, 1332–1333 (1979).

6. Garay, J., Cressman, R., Xu, F., Varga, Z. & Cabello, T. Optimal forager against ideal free distributed prey. *Am. Nat*. **186**, 111-122 (2015a).

7. McNair, J.N. A stochastic foraging model with predator training effects: I. Functional response, switching, and run lengths. *Theor. Pop. Biol*. **17**, 141-166 (1980).

8. Foglar H., Malausa J.C. & Wajnberg E. The functional response and preference of *Macrolophus caliginosus* (Het.: Miridae) for two of its prey: *Myzus persicae* and *Tetranychus urticae*. *Entomophaga* **35**, 465-474 (1990).

9. Jones, T.S., Bilton A.R., Mak L. & Sait M. Host switching in a generalist parasitoid: contrasting transient and transgenerational costs associated with novel and original host species. *Ecol. Evol*. **5**, 459-465 (2015).

10. Cabello T., Rodriguez-Manzaneque M.A. & Gallego J.R. Can predators' pheromones modulate the response to herbivore-induced plant volatiles? *Ann. Appl. Biol*. **170**, 369-378. (2017).

11. Cressman, R., Krivan, V. & Garay, J. Ideal free distributions, evolutionary games, and population dynamics in multiple-species environments. *Am. Nat*. **164**, 473-489 (2004).

12. Garay J. & Varga Z. Survivor's dilemma: Defend the group or flee? *Theor. Pop. Biol*. **80**, 217-225 (2011).

13. Cressman, R. & Garay, J. The effects of opportunistic and intentional predators on the herding behavior of prey. *Ecology* **92**, 432-440 (2011).

14. Cressman, R. & Garay, J A Predator-Prey Refuge System: Evolutionary Stability in Ecological Systems. *Theor. Pop. Biol*. **76**, 248-257 (2009).

15. Broom, M., Luther, R.M., Ruxton, G.D. & Rychtár, J. A game-theoretic model of kleptoparasitic behavior in polymorphic populations. *J. Theor. Biol*., **255**, 81-91. (2008).

16. Broom M. & Rychtar, J. *Game-Theoretical Models in Biology*. (Chapman & Hall/CRC 2013).

17. Garay J., Varga Z., Gámez M. & Cabello T. Functional response and population dynamics for fighting predator, based on activity distribution. *J. Theor. Biol*. **368**, 74-82 (2015b).

18. Garay, J., Varga Z, Cabello T. & Gamez M. Optimal nutrient foraging strategy of an omnivore: Liebig's law determining numerical response. *J. Theor. Bio*. **310**, 31-42 (2012).

19. Stephens, D.W. Krebs J.R. *Foraging Theory* (Princeton University Press 1987).

20. Fernandez-Maldonado F.J., Gallego J.R., Valencia A., Gamez M., Varga Z., Garay J. & Cabello T. Cannibalism: Do risks of fighting and reprisal reduce predatory rates? *Community Ecol*. **18**, 87-96 (2017).

21. Punzalan, D., Rodd, F.H. & Hughes, K.A. Perceptual processes and the maintenance of polymorphism through frequency-dependent predation. *Evol. Ecol*. **19**, 303-32 (2005).

22. Symondson, W.O.C., Sunderland, K.D. & Greenstone, M.H. Can generalist predator be effective biocontrol agents? *Annu. Rev. Entomol*. **47**, 561-594 (2002).

23. Gillespie, D.R. & Roitberg, B.D. Inter-guild influences on intra-guild predation in plant-feeding omnivores In *Trophic and Guild Interactions in Biological Control* (eds. Brodeur J. & Boivin G) 71-100 (Springer, 2006).

24. Vila, E. & Cabello, T. 2014. Biosystems engineering applied to greenhouse pest control. In *Biosystems engineering: biofactories for food production in the XXI century* (eds. Torres I. & Guevara R.) 99-128 (Springer 2014).

25. Coll, M. & Guershon M. Omnivory in terrestrial arthropods: mixing plant and prey diets. *Annu. Rev. Entomol*. **47**, 267-297 (2002).

26. McMurtry, J.A. & Croft, B.A. Lifestyles of phytoseiid mites and their roles in biological control. *Annu. Rev. Entomol*. **42**, 291-321 (1997).

27. Hurd, L.E. (2008) Predation: the role of generalist predators in biodiversity and biological control In *Encyclopedia of entomology* (Ed. Capinera, J.L.) 3038-3042 (Springer 2008).

28. Cabello, T., Gallego, J.R., Fernandez, F.J., Gamez, M., Vila, E., Pino, M. & Hernandez-Suarez, E. (2012). Biological control strategies for the south american tomato moth in greenhouse tomatoes. *J. Econ. Entomol.* **105**, 2085-2096 (2012).

29. Bompard, A., Jaworski, C.C., Bearez, P. & Desneux, N. Sharing a predator: can an invasive alien pest affect the predation on a local pest? *Popul. Ecol*. **55**, 433-440 (2013).

30. Jaworski, C.C., Bompard, A., Genies, L., Amiens-Desneux, E. & Desneux, N. (2013) Preference and prey switching in a generalist predator attacking local and invasive alien pests. *PLoS ONE* **8**, e82231. doi:10.1371/journal.pone.0082231 (2013).

31. Koss A.M. & Snyder W.E. Alternative prey disrupt biocontrol by a guild of generalist predators. *Biol. Control* **32**, 243-251 (2005).

32. MacRae, I.V. & Croft, B.A. Intra- and interspecific predation by adult female *Metaseiulus occidentalis* and *Typhlodromus pyri* (Acari: Phytoseiidae) when provisioned with varying densities and ratios of *Tetranychus urticae* (Acari: Tetranychidae) and phytoseiid larvae. *Exp. Appl. Acarol*. **21**, 235-245 (1997).

33. Wade, M.R., Zalucki, M.P. & Franzmann, B.A. Influence of observer presence on Pacific damsel bug behavior: who is watching whom? *J. Insect Behav*. **18**, 651-667 (2005).

34. Canon. *Communication Software for the Camera EOS Utility*, Version 2.14. (Canon Inc. 2014)

35. Schneider, C.A., W.S. Rasband & Eliceiri, K.W. NIH Image to Image: 25 years of image analysis. *Nat. Methods* **9**, 671-675 (2012).

36. Manly, B.F.J., Miller, P. & Cook, L. Analysis of a selective predation experiment. *Am. Nat*. **106**, 719-736 (1972).

37. Cock, M. The assessment of preference. *J. Anim. Ecol*. **47**, 805-816 (1978).

38. Sherratt, T. & Harvey, I. Frequency-dependent food selection by arthropods: a review. *Biol. J. Linn. Soc.* **48,** 167-186 (1993).