
ELSEVIER
Journal of
Theoretical
Biology

Journal of Theoretical Biology 310 (2012) 31–42

Contents lists available at SciVerse ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

Optimal nutrient foraging strategy of an omnivore: Liebig's law determining numerical response

József Garay [a,*], Zoltán Varga [b], Tomás Cabello [c], Manuel Gámez [d]

[a] Research Group of Theoretical Biology and Evolutionary Ecology of the Hungarian Academy of Sciences and Department of Plant Systematics, Ecology and Theoretical Biology, L. Eötvös University, Pázmány P. sétány 1/C, H-1117 Budapest, Hungary
[b] Institute of Mathematics and Informatics, Szent István University, Páter K. u. 1., H-2103 Gödöllő, Hungary
[c] Department of Applied Biology, University of Almería, Ctra. Sacramento s/n, ES-04120 Almeria, Spain
[d] Department of Statistics and Applied Mathematics, University of Almería, La Cañada de San Urbano s/n, 04120 Almeria, Spain

HIGHLIGHTS

- We build a bridge between stoichiometric ecology and optimal foraging models.
- Give a theoretical explanation of a bistable coexistence observed in omnivory.
- Our model includes different biological mechanisms at a time.
- May find application in nutritional ecology, intraguild predation and pest control.

ARTICLE INFO

Article history:
Received 5 May 2012
Received in revised form
14 June 2012
Accepted 15 June 2012
Available online 28 June 2012

Keywords:
Ecological stoichiometry
Imperfectly substitutable resources
Liebig's Law
Numerical response
Omnivory

ABSTRACT

The paper is aimed at a theoretical explanation of the following phenomenon. In biological pest control in greenhouses, if an omnivore agent is released before the arrival of the pest, the agent may be able to colonize, feeding only on plant and then control its arriving prey to a low density. If the pest arrives before the release of the agent, then it tends to reach a high density, in spite of the action of the agent. This means that according to the initial state, the system displays different stable equilibria, i.e. bistable coexistence is observed. Based on the biological situation, the explaining theoretical model must take into account the stoichiometry of different nutrients and the optimal foraging of the omnivore agent. We introduce an optimal numerical response which depends on the optimal functional responses and on the 'mixed diet–fitness' correspondence determined by 'egg stoichiometry', in our case by Liebig's Law; moreover we also study the dynamical consequences of the latter when the plant is "inexhaustible". In our model, we found that under Holling type II functional response, the omnivore–prey system has a unique equilibrium, while for Holling type III, we obtained bistable coexistence. The latter fact also explains the above phenomenon that an omnivore agent may control the pest to different levels, according to the timing of the release of the agent.

1. Introduction

1.1. The theoretical problem

The basic experimental motivation of our present study is a phenomenon observed in greenhouses, where an omnivore agent feeding only on a plant, reached a lower population density than in case of living on a mixed diet. If this agent is released before the arrival of the pest, the agent may be able to colonize and then control the arriving pest to a low density. If the pest arrives before the release of the agent, then it tends to reach a high equilibrium density, in spite of the action of the agent. At theoretical level this means that according to the initial state, the system displays different stable equilibria, i.e. bistable coexistence is observed.

In greenhouse tomato crops, for instance, the phytophagous spider mites (*Tetranychus urticae* Kock) (Acari: Prostigmata: Tetranychidae) and its omnivore predator – *Phytoseiulus persimilis* Athias-Henriot (Acari: Mesostigmata: Phytoseiidae), also feeding on pollen – are a good example for the above phenomenon (Gerson et al., 2003).

In the considered biological situation, for a general theoretical model, the following three mechanisms must be taken into account: stoichiometry, optimal foraging and population dynamics based on functional response.

1.1.1. Stoichiometry

In many cases mixed diet can improve the fitness of consumers (see e.g. Raubenheimer et al., 2009; Groenteman et al., 2006; Bilde

* Corresponding author. Tel.: +36 1 3722500/8798; fax: +36 1 3812188.
E-mail addresses: garayj@caesar.elte.hu (J. Garay), Varga.Zoltan@gek.szie.hu (Z. Varga), tcabello@ual.es (T. Cabello), mgamez@ual.es (M. Gámez).

0022-5193/$ - see front matter © 2012 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.jtbi.2012.06.021