



## Original Research Article

## Remarks on the number of persistent states to a fragmented predator–prey model system

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## ABSTRACT

We consider a predator–prey model system for spatially distributed species over patches. Each predator species has a unique preferred patch (shelter and reproduction site) and travel for chasing prey. Its individuals are split into resident from the preferred patch and travelers. Further there is at most one resident predator species per patch. Depending on the availability of local anthropized resources not related to local prey on the preferred patch, one distinguishes between well-fed and starving predators. We assume prey species do not disperse at the predator scale.

In this study we are interested in the number of persistent stationary states for the resulting ordinary differential equations model system. There exists at most one persistent predator–prey stationary state when there is exactly one starving resident predators per patch provided all functional responses to predation are Lotka–Volterra like or when a single starving resident predators is available. Else multiple persistent predator–prey stationary state are likely to exist. A specific emphasis is put on toy-model systems with 2 or 3 patches. Slow–fast dynamical methodology is also used for locally asymptotically stable purposes.

Numerical experiments suggest that several scalings may govern the dynamics at stabilization.

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## 1. Introduction

In this study we are interested in a specific heterogeneous predator–prey model system posed on a fragmented spatial domain made of  $N \geq 2$  patches.

Our motivation lies in previous works on *Toxoplasma gondii*, cf. Langlais et al. (2012), L  lu et al. (2013) and L  lu et al. (2010), wherein the underlying predator–prey system exhibited quite complex and interesting features having a strong impact on *T. gondii* persistence.

Heterogeneity comes from anthropization of the environment. Typically patches represent urban or sub-urban areas, villages, farms or fields. Prey are small rodents or birds with variable local abundance, not dispersing at the predator scale. Predators are domestic cats, *Felis catus*, having either abundant or scarce sustainable local food supply not related to hunting within a preferred patch they belong to. Predators disperse through the spatial domain for chasing additional prey. This led us to introduce well-fed and starving predator non mixing species as well as to

consider resident and traveling predators similarly to host populations for epidemic models in Arino and van den Driessche (2006).

A complex predator–prey model system made of a set of ordinary differential equations (ODE) taking into account these features was devised in Langlais et al. (2012). A few cases were analyzed there for Lotka–Volterra functional responses to predation, with  $N = 3$  patches and at most one starving predator species. The goal was to shed some light on *T. gondii* spatial spread in such an environment.

In the present work we come back to this complex predator–prey model system assuming functional responses to predation can take both usual parametric forms, Lotka–Volterra and Holling type II.

In order to have a more consistent model we modified prey and well-fed predators dynamics. Instead of assuming conventional logistic dynamics,  $v' = (r - kv)v$ , based on a growth rate,  $r$ , and a carrying capacity,  $r/k$ , we chose modified dynamics,  $v' = \Lambda - av$ , based on resources,  $\Lambda$ , and consumption,  $a$ .

In field, farm, village, suburban and urban areas available resources for rodent populations are quite contrasted in abundance and rely on the anthropization of the environment, cf. Deplazes et al. (2004). Rodent population size depends on local available resources. It becomes quite realistic to assume its subsequent dynamics is governed by available resources ( $\Lambda$ ) and per capita consumption

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(a) rather than by a growth rate and a carrying capacity. This is also adequate for domestic cats sufficiently fed by their owners, well-fed cats in the sequel. For insufficiently fed cats, starving cats in the sequel, predation on a preferred patch or on nearby ones will supply additional non anthropized resources.

This slightly simplifies the analysis while preserving its main feature: dynamical complexity measured via the number of semi-trivial and persistent stationary states increases with either the choice of Holling type II functional responses to predation or the number of patches.

This main feature is also related to a quite ancient set of questions. First find sufficient conditions to ensure the existence of a persistent state in a multi-species/multi-patch population dynamics model system, cf. Gopalsamy (1984), Gopalsamy and Ahlip (1983), Kaykobad (1985) and Kaykobad (1985). Second analyze local or global stabilities, cf. Kuang and Takeuchi (1994), Li and Shuai (2010) and references therein.

Given the size of our model system, even for  $N = 2, 3$ , stability analysis of semi-trivial and persistent stationary states becomes quite complicated to handle. Unfortunately the general methodology devised in Li and Shuai (2010) does not seem to apply.

To go around this we got help from a general methodology related to slow–fast dynamics allowing to reduce the size of the system, cf. Auger et al. (2008), Auger et al. (2012), Nguyen-Ngoc et al. (2012), Marva et al. (2012) and references therein. Actually not all processes occur at the same scale: predation and demography for prey and predator species are much slower processes than traveling for predators. This allowed us to give local asymptotic stability (LAS) results for semi-trivial stationary states, unfortunately not for persistent ones. Global asymptotic stability (GAS) results are mostly open problems.

The main concern of this study remains the number of persistent stationary states. From our model well-fed predators have independent dynamics and do not pose any problem, complexity coming both from starving predator species and functional responses to predation.

For  $N \geq 2$  patches the simplest case arises when there is exactly one starving resident predator species per patch, all functional responses to predation being of Lotka–Volterra type: one gets 0 or 1 persistent stationary state.

Else multiplicity of persistent stationary state is likely to occur for a suitable parameter data set as soon as one considers a system made of either  $2 \leq N_{\max} < N$  starving resident predator species, regardless functional responses to predation, or  $2 \leq N_{\max} \leq N$  starving resident predator species with at least one functional responses to predation being of Holling type II.

Our work is organized as follows. In Section 2 we derive our model system. Main assumptions, notations and definitions used in this study are listed Section 3. In Section 4 we give a summary of our main results. Section 5 is dedicated to generic results independent of the number  $N$  of patches. In Sections 6 and 7 we analyze the case of Lotka–Volterra functional responses to predation for 2 or 3 patches. Section 8 is dedicated to 2 patches and at least one functional responses to predation being of Holling type II. In Section 9 we discuss our main results and offer some perspectives of development.

## 2. A dedicated predator–prey model system

Our fragmented spatial domain is made of  $N \geq 2$  patches,  $(\mathcal{P}_n)_{1 \leq n \leq N}$ .

One assumes a single (aggregated) prey species per patch  $\mathcal{P}_n$  whose density,  $V_n$ , follows a logistic-like dynamic in a predator free environment

$$V'_n = \Lambda_n^v - a_n^v V_n, \quad a_n^v > 0, \quad \Lambda_n^v > 0 \tag{2.1}$$

yielding a carrying capacity  $(\Lambda_n^v/a_n^v)$ . Prey species do not migrate between patches.

On a given patch,  $\mathcal{P}_n$ , several predator species may be found

*resident predator species*, whose individuals spend most of their life span there:  $\mathcal{P}_n$  is a shelter for all its individuals and a site for species reproduction. Resident predators prey on local prey in patch  $\mathcal{P}_n$  and travel to chase prey from patch  $\mathcal{P}_j$  while reproduction occurs only in this preferred patch  $\mathcal{P}_n$ ;

*temporary predator species*, whose individuals belong to a resident species from patch  $\mathcal{P}_\ell$  traveling at a rate  $c_{\ell n}^\ell$  to patch  $\mathcal{P}_n$  for a short time span and coming back at a rate  $c_{n\ell}^\ell$  to its preferred patch  $\mathcal{P}_\ell$  thereafter.

A predator species can only be a resident species in one patch. One assumes at most one resident predator species per patch,  $N_{\max}$  patches hosting a resident predator species,  $1 \leq N_{\max} \leq N$ .  $U_{nn}$  is the density of resident predators from patch  $\mathcal{P}_n$  currently in patch  $\mathcal{P}_n$ , while  $U_{nj}$  is the density of resident predators from patch  $\mathcal{P}_n$  visiting patch  $\mathcal{P}_j$ .

For  $n = 1, \dots, N_{\max}$  predator species  $(U_{nj})_{1 \leq j \leq N}$  is termed a

*well-fed predator species*, provided an abundant anthropized food supply not related to chasing prey,  $\Lambda_n^u \gg 0$ , is available in the preferred patch  $\mathcal{P}_n$ ;

*starving predator species*, when a reduced food supply not related to chasing prey is available in the preferred patch  $\mathcal{P}_n$ ,  $\Lambda_n^u \approx 0$ .

Let  $p, 0 \leq p \leq N_{\max}$ , be the number of well-fed predator species, labelled from  $n = 1$  to  $p$  when  $p > 0$ , so that  $q = N_{\max} - p$  is the number of starving predator species, labelled from  $n = p + 1$  to  $N_{\max}$  when  $p < N_{\max}$ .

In absence of dispersal and prey on patch  $\mathcal{P}_n$  a well-fed resident predator density  $U_{nn}$  follows a logistic-like dynamic, predation having a negligible impact on its food supply, while a starving resident predator density will experience an exponential decay. Temporary predator species,  $U_{nj}$ , have an additional mortality rate,  $a_{nj}^u$ , while visiting patch  $\mathcal{P}_j$ .

On each patch  $\mathcal{P}_n$  resident and temporary predators,  $(U_{\ell n})_{1 \leq \ell \leq N_{\max}}$ , chase local prey,  $V_n$ . Functional responses to predation,  $\pi_{\ell n}$ , of  $U_{\ell n}$  read,

$$\pi_{\ell n}(V_n) = \frac{e_{\ell n} V_n}{1 + h_{\ell n} e_{\ell n} V_n}, \quad e_{\ell n} \geq 0, \quad h_{\ell n} \geq 0, \tag{2.2}$$

$\ell = 1, \dots, N_{\max}, n = 1, \dots, N$ . Accordingly  $\varepsilon_{\ell n} \pi_{\ell n}(V_n)$  is the numerical response to predation with  $(\varepsilon_{\ell n} \geq 0)_{1 \leq \ell \leq N_{\max}, 1 \leq n \leq N}$  the conversion rate of the biomass of captured and eaten prey into a birth rate for predator species. A Lotka–Volterra functional response to predation corresponds to a  $h_{\ell n} = 0$  while a positive  $h_{\ell n}$  provides a Holling type II functional response to predation.

A predator–prey model system with a set of up to  $(N \times N_{\max} + N)$  ordinary differential equations can be derived. For predator species  $(U_{nj})_{1 \leq n \leq N}$  it reads

$$V'_j = \Lambda_j^v - a_j^v V_j - \sum_{1 \leq \ell \leq N_{\max}} \pi_{\ell j}(V_j) U_{\ell j}, \quad j = 1, \dots, N; \tag{2.3}$$

$$U'_{nn} = \Lambda_n^u + \sum_{1 \leq j \leq N} \varepsilon_{nj} \pi_{nj}(V_j) U_{nj} - a_{nn}^u U_{nn} - \sum_{1 \leq j \leq N, j \neq n} c_{jn}^n U_{nn} + \sum_{1 \leq j \leq N, j \neq n} c_{jn}^n U_{nj}; \tag{2.4}$$

$$U'_{nj} = -a_{nj}^u U_{nj} - c_{jn}^n U_{nj} + c_{jn}^n U_{nn}, \quad j = 1, \dots, N, \quad j \neq n. \tag{2.5}$$

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