

How predator food preference can change the destiny of native prey in predator–prey systems

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Abstract

The aim of this work is to develop and analyse a mathematical model for a predator–2 preys system arising in insular environments. We are interested in the evolution of a native prey population without behavioural traits to cope with predation or competition, after the introduction of alien species. Here, we consider a long living bird population with low fertility rate. We point out the effects of the preference of the predator for either juvenile or adult stages. In addition, we study the impact of alien prey introduction in such a model. We use a reaction-diffusion system with a singular logistic right hand side. The aim of this work is to bring interesting dynamics to the fore. As a first example, oscillatory behaviour takes place in the model without alien preys and when predators have an average preference coefficient. Introduction of alien preys can lead to species extinction.

Introduction

The invasion of oceanic islands by alien predators has proven in many cases to have significant, even disastrous effects on the native avifauna (reviews in Atkinson 1985; Veitch 1985; Keitt et al. 2002). Among mammals, the domestic cat (*Felis catus* L.) is one of the most threatening species because of its opportunistic diet behaviour (Stattersfield and Capper 2000). Predators are naturally absent in these ecosystems and most seabird species share life-history and behavioural traits, which make them especially vulnerable to alien predators (Lack 1968; Moors et al. 1992). This is particularly reinforced for seabirds, which show absolute fidelity to their breeding island (review in Bried and Jouventin

2002). Seabirds are long-lived and have a low fecundity, the extreme being a single-egg clutch without replacement; the dynamics of their population is then extremely sensitive to a small increase in adult mortality (Weimerskirch et al. 1987; Bried and Jouventin 2002). The impact of introduced predators on the native avifauna is the most dramatic on islands where alien preys have also been introduced (Atkinson 1985; Weimerskirch et al. 1989). Most seabird species spend the non-breeding period at sea. Therefore, introduced preys like rabbits (*Oryctolagus cuniculus*) and rodents (*Mus musculus* or *Rattus* sp.) represent the essential of the diet of cats in winter (Weimerskirch et al. 1989; Pontier et al. 2002). Because of their opportunistic behaviour and the ease with which birds can be captured,

cats take birds preferentially during the summer when tens of thousands of them attend their colony to breed (Bloomer and Bester 1990). However, the sensitivity to predation may vary among seabird species. Depending on bird body size and burrow size, cats preferentially prey upon either chicks or adults, or on all categories (Derenne 1976). Therefore, the consequences for seabird population dynamics should differ among species. Moreover, species are not always distributed in the same way on the island and this is especially true for large islands like the main island of Kerguelen archipelago. Generally, seabird colonies are mainly present along the coast line, whereas rabbits and rodents can settle and develop on a larger part of the island. Such heterogeneity may allow cats to reach remote bird colonies. Because of the complexity of the situation, the long term consequences of alien species introduction on the native seabird species population dynamics have to be analysed via mathematical models.

In previous works (Gaucel and Langlais 2002; Gaucel et al. 2005), a mathematical model has been developed to model the interactions between a native prey and alien predators and preys in insular environments, taking into account the spatial heterogeneity in the habitat. Problems of persistence and extinction of species have been studied in Gaucel and Langlais (2002), and invasion processes have been analysed in Gaucel et al. (2005).

In this paper we extended the unstructured model of Courchamp and Sugihara (1999) to the case of an alien predator preying on a native species split into two age stages: juveniles and adults; along the same line, we derive a predator-2 prey (alien and native) species model for an age-structured prey population based on Courchamp et al. (1999).

The models devised in the present work use predator-prey ratio instead of prey density (see Arditi and Berryman 1991 for the unstructured case). It is simplified, e.g., it does not include realistic predator functional response (see Cantrell and Cosner 1993, 2003; Fagan et al. 1999; Murray 2002). To take the spatial structures into account, we use a reaction-diffusion system. In the spirit of the model in Gaucel et al. (2005) and along the lines of Shigesada and Kawasaki

(1997), we develop a spatially structured model for a predator population preying on both an alien prey population and a native one. The native prey population is split into two stages (juveniles and adults), these stages being preyed on at different rates by the predator.

Next we perform numerical simulations to analyse the invasion problem for a long living native prey population with a low fertility rate in the presence of introduced preys and predators. We consider a native population living in two favourable zones, one being easily reachable by alien species, the second being isolated from alien predators by an intermediate zone; this latter zone is taken as hostile for native preys but as a hospitable habitat for the alien preys. So, as in Gaucel et al. (2005), we have to consider the buffer role played by the alien prey population in the invasion process by the predator.

We first describe the predator-prey system behaviour when the predator population has a strong preference for one of the two age stages of the prey population. Comparing these results to those in Gaucel et al. (2005), we show how the age structure in the prey population can modify the dynamics of this population. We also exhibit how the preying preference of the alien predator on either juvenile or adult stages of the native prey population affects the dynamical behaviour of both native and introduced population densities. Finally, we run simulations to analyse the invasion process in presence of an introduced prey.

Mathematical models

In the first subsection we briefly describe a mathematical model for an unstructured predator-2 preys system in insular environment based on earlier works (Courchamp and Sugihara 1999; Courchamp et al. 1999; Gaucel et al. 2005). In the second subsection we first present a simple model for a prey population split into two age stages; we give a condition for the persistence of the prey population. Next we develop a predator-prey model with age stage structure for the prey population based on the unstructured model in Gaucel et al. (2005); we perform a quick mathematical analysis, exhibiting the main

features of this model, i.e., a possibility of finite or infinite time extinction of species, coexistence or periodic dynamics. The last subsection deals with the development of our spatially structured model for this predator-2 preys system with two age stages in the prey population.

Unstructured models for a predator-competitor-prey system

First let us introduce the original model from Courchamp and Sugihara (1999). State variables are B , the prey density, and C , the predator density. Let $K > 0$ be the carrying capacity of the insular environment; let $r_b > 0$ and $r_c > 0$, be the net growth-rate of the prey and predator populations. Introducing $\mu > 0$, the annual individual intake of preys per predator, the carrying capacity of the introduced predator population is B/μ . The model reads

$$\begin{cases} B' = r_b(1 - B/K)B - \mu C, & B(0) > 0, \\ C' = r_c(1 - \mu C/B)C, & C(0) > 0. \end{cases} \quad (1)$$

Three stationary states with non-negative entries are found for (1): $(0,0)$, $(K, 0)$, and $(B^* = \frac{r_b-1}{r_b}K, C^* = \frac{B^*}{\mu})$ provided $r_b > 1$; $(K, 0)$ is always unstable. The dynamics of solutions to (1) can be depicted using Figure 1, see Gaucel et al. (2005). Persistence of both populations always occurs when $r_b > 1$ and $r_c > 1$. Extinction of both populations occurs in infinite time when $r_b < 1$ and $r_c > 1$; it also occurs in finite time for $0 < r_b < r_c < 1$, i.e., there exists a finite time $T = T(B(0), C(0))$ such

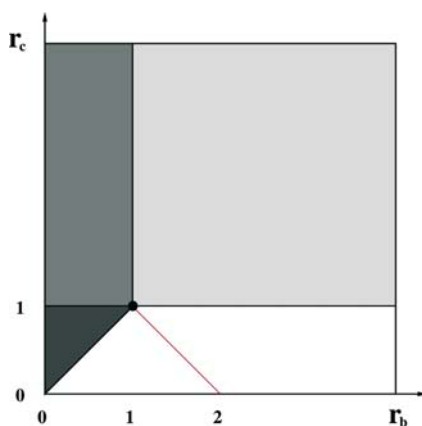


Figure 1. Bifurcation diagram for the possible dynamics of solutions to (1).

that $B(t) \rightarrow 0$ and $C(t) \rightarrow 0$ as $t \rightarrow T(B(0), C(0))$. In the rest of the parameter space, i.e. for $r_c < 1$ and $r_b > r_c$, the dynamical behaviour depends on the initial data $B(0)$ and $C(0)$. For $r_c < r_b$ and $r_b + r_c < 2$, one gets extinction of both populations in either finite or infinite time. Moreover, for $r_b + r_c > 2$ and $r_c < 1$, (B^*, C^*) is locally asymptotically stable, so one can get extinction in finite or infinite time, or persistence of both populations. See Gaucel et al. (2005) for details.

Now we modify the previous model, adapting it to a three species predator-competitor-prey system. The model is derived in Courchamp et al. (1999). State variables are, B , the native prey density, R , an introduced prey density, and, C , the alien predator density, having for respective natural growth-rates, r_b, r_r and r_c . Let, K_b and K_r be the carrying capacities of preys B and R . Let μ_b and μ_r be the annual individual intake of preys B and R per individual predator, so that the carrying capacity of predators become $B/\mu_b + R/\mu_r$. Parameter η represent the indirect and asymmetrical effect of the alien prey on the native one (see Courchamp and Sugihara 1999; Gaucel et al. 2005). Finally, let us introduce a preference coefficient, $\alpha > 0$, for native preys over alien ones, dealing with the flexibility and opportunism of cat population. The model reads

$$\begin{cases} B' = r_b(1 - B/K_b)B - \eta BR - \frac{\alpha B}{\alpha B + R}\mu_b C, & B(0) > 0, \\ R' = r_r(1 - R/K_r)R - \frac{R}{\alpha B + R}\mu_r C, & R(0) > 0, \\ C' = r_c \left(1 - \mu_b \mu_r \frac{C}{\mu_b R + \mu_r B} \right) C, & C(0) > 0. \end{cases} \quad (2)$$

Three unstable stationary states without predators exist: $(K_b, 0, 0)$, $(0, K_r, 0)$ and $((1 - \eta \frac{K_r}{r_b})K_b, K_r, 0)$. Two stationary states with a single prey population are found. The first one, $(\frac{r_b-1}{r_b}K_b, 0, \frac{1}{\mu_b} \frac{r_b-1}{r_b}K_b)$, is feasible if $r_b > 1$ and (LAS) provided $r_b + r_c > 2$ and $r_r < \frac{1}{\alpha} \frac{\mu_r}{\mu_b}$; the second one, $(0, \frac{r_r-1}{r_r}K_r, \frac{1}{\mu_r} \frac{r_r-1}{r_r}K_r)$, is feasible if $r_r > 1$ and (LAS) provided $r_r + r_c > 2$ and $r_b < \alpha \frac{\mu_b}{\mu_r} + \eta \frac{1}{\mu_r} \frac{r_r-1}{r_r}K_r$. See Courchamp et al. (1999) for details.

Finite time extinction for (B, R, C) always occurs when $0 < \max(r_b, r_r) < r_c < 1$ (see Gaucel et al. 2005). Conversely, no finite time extinction

for (B, R, C) may occur when $r_c > \frac{(\mu_b + \mu_r)^2}{4\mu_b\mu_r}$. Intermediate dynamics take place when either $r_c < 1$ and $\max(r_b, r_r) > r_c$ or $1 < r_c < \frac{(\mu_b + \mu_r)^2}{4\mu_b\mu_r}$.

Models with two age stages

The goal of this subsection is to derive a model in the spirit of (1) and (2), with two age stages in the prey population.

Age structured model for the prey population

State variables are J , the juvenile prey density, and A , the adult prey density for natural fertility rate, $b > 0$, and for respective natural mortality rates, $m_j > 0$ and $m_a > 0$. Introduce $\tau > 0$, the maturation rate for juvenile population or the inverse of the duration of the juvenile stage. Finally, let $k_j > 0$ and $k_a > 0$ determine the logistic pressure effect. The model reads

$$\begin{cases} J' = bA - (m_j + k_j(A + J))J - \tau J, & J(0) > 0, \\ A' = \tau J - (m_a + k_a(A + J))A, & A(0) > 0. \end{cases} \quad (3)$$

It preserves non-negativity of state variables A and J .

To perform the stability analysis, we introduce the total population density, $P^* = A^* + J^*$, (A^*, J^*) being a stationary state with non-negative components. After some algebra, we have

$$P^* \left[k_a k_j P^{*2} + (k_a(\tau + m_j) + k_j m_a) P^* + m_a(\tau + m_j) - \tau b \right] = 0 \quad (4)$$

So system (3) has two stationary states, $(0, 0)$, and a positive state

$$J^* = \frac{bP^*}{\tau + b + m_j + k_j P^*}, A^* = \frac{\tau P^*}{\tau + m_a + k_a P^*} \quad (5)$$

which exists if and only if

$$1 < \frac{\tau}{m_j + \tau} \frac{b}{m_a}. \quad (6)$$

Under condition (6), (J^*, A^*) is locally asymptotically stable, $(0, 0)$ is unstable; else $(0, 0)$ is locally asymptotically stable. For demographic coefficients, b, m_j, m_a and τ , one can use field data published in literature. Finally, Figure 2 depicts the elasticity of the stationary state (J^*, A^*) with respect to the demographic parameters given in Table 1. The natality rate b and the maturation rate τ have the higher impact on the sizes, J^* and A^* , of juvenile and adult preys at equilibrium. The parameters k_a and k_j associated to the logistic effect have a smaller impact than τ and b . Finally, the mortality rates m_a and m_j have insignificant effects on (J^*, A^*) .

Age structured model for a predator–prey system

Using model (3), we now want to build a mathematical model for a predator–prey system with age stages for the prey population. We consider an alien predator population with a density C and

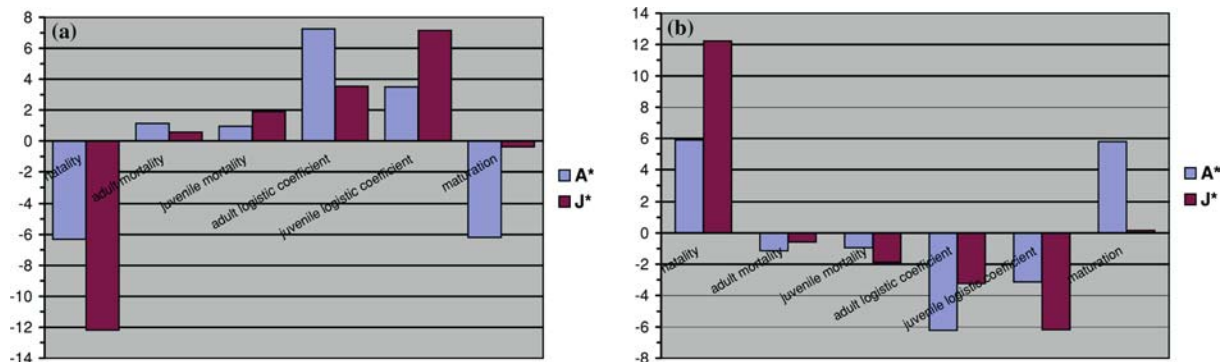


Figure 2. Elasticity analysis for 6 parameters of the model for a prey population split into two age stages, in (3), using a variation of -10%, (a), and +10%, (b), around the values given in Table 1. We present the impact on the non-trivial stationary state (A^*, J^*) , see (5).

Table 1. Set of parameter values for a long living species of native preys (upper table) and two alien species (lower table): (in), (inter) and (out) are respectively for the inner zone, the intermediate zone and the outer one.

Juvenile native preys					Adult native preys			
	m_j	k_j	τ	μ_j	b	m_a	k_a	μ_a
(in)/(out)	0.51	$6.6 \times 10^{-4}/10^{-3}$	1	360	0.69	3×10^{-2}	$6.6 \times 10^{-5}/10^{-4}$	180
(inter)	0.69	1	1	360	0.69	5.1×10^{-2}	10	180

Alien species				
Prey	Prey			Predator
	r_r	K_r	μ_r	r_c
(in)	1.69	1	180	0.2
(inter)	1.69	15000	180	0.2
(out)	1.69	10000	180	0.2

a net growth-rate $r_c > 0$. Let $\mu_a > 0$ and $\mu_j > 0$, respectively be the annual individual intake of preys per predator for each age stage, so that the carrying capacity of predators is $A/\mu_a + J/\mu_j$. Finally, a preference coefficient, $\gamma > 0$, for juvenile preys over adult ones is introduced. The model reads

$$\begin{cases} J' = bA - (m_j + k_j(A + J))J - \tau J - \mu_j C \frac{\gamma J}{\gamma J + A}, \\ J(0) > 0, \\ A' = \tau J - (m_a + k_a(A + J))A - \mu_a C \frac{A}{\gamma J + A}, \\ A(0) > 0, \\ C' = r_c \left(1 - \mu_a \mu_j \frac{C}{\mu_j A + \mu_a J} \right) C, \quad C(0) > 0. \end{cases} \tag{7}$$

We have a system of ordinary differential equations, singular at $A = J = 0$. We have one unstable stationary state without predators : $(J^*, A^*, 0)$ where (J^*, A^*) is the stationary state of system (3), feasible if and only if condition (6) holds.

Now we study the problem of finite time extinction of solutions to (7). First, we rescale the state variables, setting $J =: \gamma^2 J$, $A =: \gamma A$, $b =: \gamma b$, $k_j =: k_j/\gamma^2$, $k_a =: k_a/\gamma^2$, $\mu_j =: \gamma^2 \mu_j$, $\mu_a =: \gamma \mu_a$, $\tau =: \tau/\gamma$. Then, using $P = A + J$ the total prey population, $\theta = A/(A + J)$ the proportion of adult preys within the total prey population and $Q = C/(A + J)$ the ratio of predator/prey as new state variables, one gets a non-singular system

$$\begin{cases} P' = [F_1(\theta, Q) - F_2(\theta)P]P, \\ \theta' = G(\theta) + \theta(1 - \theta)[m_j - m_a + \tau\gamma] \\ \quad + \theta(1 - \theta)[(\mu_j - \mu_a)Q \\ \quad + (k_j - k_a)(\gamma\theta - \theta + 1)P], \\ Q' = [H_1(\theta) + H_2(\theta)P - H_3(\theta)Q]Q. \end{cases} \tag{8}$$

in the forward invariant set, $P \geq 0$, $0 \leq \theta \leq 1$, $Q \geq 0$, wherein

$$\begin{aligned} F_1(\theta, Q) &= (\tau(1 - \gamma) - m_j - \mu_j Q)(1 - \theta) \\ &\quad + (b - m_a - \mu_a Q)\theta, \\ F_2(\theta) &= (1 + (\gamma - 1)\theta)(k_j(1 - \theta) + k_a\theta), \\ G(\theta) &= \tau(1 - \theta)^2 - b\theta^2, \\ H_1(\theta) &= r_c - [(1 - \theta)(\tau(1 - \gamma) - m_j) \\ &\quad + \theta(b - m_a)], \\ H_2(\theta) &= (\gamma\theta + 1 - \theta)(k_a\theta + k_j(1 - \theta)), \\ H_3(\theta) &= [r_c \mu_j \mu_a - (\mu_a\theta + \mu_j(1 - \theta))(\mu_a(1 - \theta) \\ &\quad + \mu_j\theta)]/(\mu_a(1 - \theta) + \mu_j\theta). \end{aligned} \tag{9}$$

A careful analysis of (9) shows that for $0 \leq \theta \leq 1$ one has $H_3(\theta) < 0$ when $r_c < 1$ and $H_1(\theta) \geq 0$ when $r_c \geq \max(\tau(1 - \gamma) - m_j, b - m_a)$ in (9). Hence, one may conclude from the third equation in (8) that finite time blow-up for Q always occurs when $0 < \max(\tau(1 - \gamma) - m_j, b - m_a) \leq r_c < 1$. So finite time extinction for (J, A, C) always occurs when $0 < \max(\frac{\tau}{\gamma}(1 - \gamma) - m_j, \gamma b - m_a) \leq r_c < 1$ in (7). Conversely, for $0 \leq \theta \leq 1$ one has $H_3(\theta) > 0$ when $r_c > \frac{(\mu_j + \mu_a)^2}{4\mu_j\mu_a}$. Hence one may conclude from the third equation in (9) that no finite time blow-up for Q may occur when $r_c > \frac{(\mu_a + \mu_j)^2}{4\mu_a\mu_j}$. So, no finite time extinction for (J, A, C) may occur when $r_c > \frac{(\mu_a + \gamma\mu_j)^2}{4\gamma\mu_a\mu_j}$.

The case of positive stationary states is more complicated. Indeed, when (6) holds, there is at least one positive stationary state but under some cir-

cumstances, system (7) can have three positive stationary states. Within the range of parameters given in Table 1, there is a unique persistent state, i.e., stationary state with positive components. It is unstable and more precisely, numerical simulations show:

- for intermediate values of γ , a stable periodic dynamic takes place,
- for either small ($0 < \gamma < \gamma_-$) or large values ($\gamma > \gamma_+$) of γ , a global extinction of both prey and predator populations occurs.

The bifurcation at $\gamma = \gamma_-$ and $\gamma = \gamma_+$ are quite fast. The amplitude and the period of the time periodic solutions of (7) are almost constant within the range $\gamma_- < \gamma < \gamma_+$. A sudden collapse arises at $\gamma = \gamma_-$ and $\gamma = \gamma_+$.

These dynamical behaviours are governed by the size of the demographic parameters b, m_j and m_a . For short living species having a large fertility rate, the oscillatory behaviour is preserved at intermediate values of γ ; for large values of γ , damped oscillations are eventually observed and the persistent state becomes stable.

A spatially and age stage structured model for heterogeneous insular environment

Let Ω be a two dimensional spatial domain. We consider spatially distributed densities, $A(\mathbf{x},t), J(\mathbf{x},t)$, of adult and juvenile native preys, and, $C(\mathbf{x},t)$, of introduced predators. Then we need spatially heterogeneous logistic coefficients, $(k_a(\mathbf{x}), k_j(\mathbf{x}))$ for preys, spatially heterogeneous diffusion rates, $(d_a(\mathbf{x}), d_j(\mathbf{x}), d_c(\mathbf{x}))$, and demographic coefficients $(b(\mathbf{x}), m_a(\mathbf{x}), m_j(\mathbf{x}))$ for the prey species, $r_c(\mathbf{x})$, the natural growth-rate for the predator species. A spatially heterogeneous model reads

$$\begin{cases} \partial J/\partial t - \text{div}(d_j(\mathbf{x})\nabla J) \\ = bA - (m_j + k_j(A + J))J - \tau J - \mu_j C \frac{\gamma J}{\gamma J + A}, \\ \partial A/\partial t - \text{div}(d_a(\mathbf{x})\nabla A) \\ = \tau J - (m_a + k_a(A + J))A - \mu_a C \frac{A}{\gamma J + A}, \\ \partial C/\partial t - \text{div}(d_c(\mathbf{x})\nabla C) \\ = r_c \left(1 - \mu_a \mu_j \frac{C}{\mu_j A + \mu_a J} \right) C, \end{cases} \tag{10}$$

supplemented by no-flux boundary conditions on the boundary $\partial\Omega$ of Ω

$$\begin{aligned} d_p(\mathbf{x})\nabla N(\mathbf{x},t) \cdot \nu(\mathbf{x}) &= 0, \quad \mathbf{x} \in \partial\Omega, \quad t > 0, \\ \text{for } N &= A, J, C, \end{aligned} \tag{11}$$

ν being the unit outward normal to $\partial\Omega$ on Ω , corresponding to isolated populations and a set of non-negative and bounded initial conditions

$$N(\mathbf{x},0) = N_0(\mathbf{x}) \geq 0, \quad \text{for } N = A, J, C, \quad \mathbf{x} \in \Omega. \tag{12}$$

A three species model is derived from (10) (11) (12), using previous works on model (2) (see Gaucel and Langlais 2002; Gaucel et al. 2005), introducing an alien competitor population $R(\mathbf{x},t)$ with parameters, $d_r(\mathbf{x})$, the diffusive rate, $K(\mathbf{x})$, the carrying capacity, $r_r(\mathbf{x})$, the natural growth-rate. As the native population is split into two age stages, the pressure of the introduced prey population is now depicted by coefficients η_j and η_a . Carrying capacity of the cat population become $\frac{A}{\mu_a} + \frac{J}{\mu_j} + \frac{R}{\mu_r}$. Because the cat is an opportunistic predator, predation terms of each prey will depend on the proportion of this prey in the total prey population. Finally, a preference coefficient, $\alpha > 0$, is introduced for native preys over alien ones. The new model reads

$$\begin{cases} \partial J/\partial t - \text{div}(d_j(\mathbf{x})\nabla J) \\ = bA - (m_j + k_j(A + J))J - \tau J \\ - \eta_j R J - \mu_j C \frac{\gamma \alpha J}{\alpha(\gamma J + A) + R}, \\ \partial A/\partial t - \text{div}(d_a(\mathbf{x})\nabla A) \\ = \tau J - (m_a + k_a(A + J))A \\ - \eta_a R A - \mu_a C \frac{A}{\alpha(\gamma J + A) + R}, \\ \partial R/\partial t - \text{div}(d_r(\mathbf{x})\nabla R) \\ = r_r \left(1 - \frac{R}{K_r} \right) R - \mu_r C \frac{R}{\alpha(A + J) + R}, \\ \partial C/\partial t - \text{div}(d_c(\mathbf{x})\nabla C) \\ = r_c \left(1 - \mu_a \mu_j \mu_r \frac{C}{\mu_j \mu_r A + \mu_a \mu_r J + \mu_a \mu_j R} \right) C. \end{cases} \tag{13}$$

supplemented by no-flux boundary conditions on the boundary $\partial\Omega$ of Ω and non-negative and bounded initial conditions (see (11) and (12)).

Numerical experiments and results

We focus on long living prey populations. The basic goal of this work was to exhibit the impact of an age stage structure in the prey population on the dynamical behaviour of a predator-prey system in heterogeneous insular environment, dealing with the preference of the predator population for either juvenile or adult preys, for a long-living prey population. At the same time, we study the predator invasion process, its dependence in the presence of an alien prey population and the effect of a successful invasion of predator population on the native prey one. Finally, we use realistic demographic parameters for an oceanic island bird population.

Spatial domain, parameter values

In Figure 3, Ω , the spatial domain is the unit square in \mathbb{R}^2 , split into three subdomains: an inner zone, an outer zone and an intermediate one. In the absence of alien species, native species, i.e., birds, have a favourable habitat in the inner and outer zones, while the intermediate zone is unfavourable. Alien preys find a favourable habitat in the outer and intermediate zones. Under some circumstances this allows the invading predator to reach the inner zone, (see Gaucel et al. 2004), to destroy the native population liv-

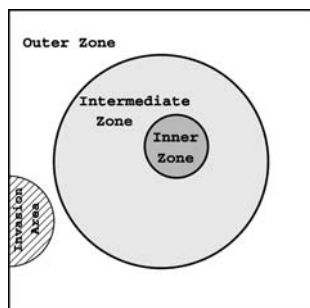


Figure 3. Spatial domain; introduced species enter the semi-circular domains located on the left side (in smaller density for the predator population).

ing there. Finally, invading species are considered to enter Ω through a tiny subdomain on the left side of the spatial domain. This last hypothesis is corroborated by the observation that in many cases rabbits and cats were introduced on islands accidentally by jumping ashore from boats or purposely by temporary settlers.

For our numerical experiments we use the set of parameters depicted in Tables 1 and 2. Long living species are characterised by a low fertility rate, b , and a long life expectancy, $\frac{1}{\tau} + \frac{1}{m_a}$, $\frac{1}{\tau}$ corresponding to the duration of the juvenile stage and $\frac{1}{m_a}$ corresponding to the duration of the adult stage. Spatial heterogeneity is characterised by different values for some parameters in the different zones in Figure 3. For the native prey population, favourable zones are described by low logistic coefficients k_a and k_j , unfavourable ones by higher logistic coefficients. Indeed, at equilibria, we have from (3) and (5)

$$k_j = \frac{bA^* - (m_j + \tau)J^*}{J^*(A^* + J^*)}, \quad k_a = \frac{\tau J^* - m_a A^*}{A^*(A^* + J^*)} \tag{14}$$

For the alien prey population, a high carrying capacity K_r correspond to a favourable zone and a low carrying capacity induce that the corresponding zone is unfavourable.

Parameters η_a and η_j are set to zero and the preference coefficients, α for the preference of predators for native prey under introduced prey, γ for the preference of predators for the juvenile stage under the adult one in the native prey population, will vary with the numerical experiments. Finally, the diffusivity coefficients of the adult and juvenile stages of the prey population, i.e. d_a and d_j , are equal, correlating the link between the movements of adult and juvenile stages.

Table 2. Set of parameter values for diffusive coefficients for the numerical simulations on models (11) and (13): (in), (inter) and (out) are respectively for the inner zone, the intermediate zone and the outer one. Low values in the intermediate zone ensure that the inner zone is isolated.

Diffusive coefficients				
	d_j	d_a	d_r	d_c
(out)	10^{-3}	10^{-3}	10^{-3}	10^{-3}
(in)/(inter)	10^{-5}	10^{-5}	10^{-5}	10^{-5}

Two species invasion numerical results

We begin with a two species prey-predator model, birds and cats, this is (10) (11) (12).

Initial conditions (12) are depicted in Figure 4, at time $t = 0$, a few cats are invading Ω through the left side.

Our first numerical simulation deals with the case of cat preference for juvenile prey populations, i.e. $\gamma > 1$, in a long living prey population; it shows an oscillatory behaviour for both prey and predator population densities in the outer zone, birds remaining absent from the intermediate zone for small diffusion coefficients. Consequently, cats cannot settle in this intermediate zone and survive to eventually invade the inner zone where they would coexist with birds or induce extinction of both predator and prey populations. Hence, invasion of the inner zone fails for cats. In Figure 5 the transient behaviour of the model is depicted; at later times, maintained oscillations are observed with a long period, about 150 years.

Next, we focus on the dynamic in the outer zone. We study the trajectories in the (A, J) and (C, P) phase planes, where $P = A + J$ is the total prey population. The trajectories described in Figure 6 first show that juvenile and adult prey populations are correlated; next, in the (C, P) phase plane, the trajectories have a periodic dynamic.

Note that this periodic dynamical behaviour is also observed for different initial values for the bird population, provided that we consider a large prey population and the introduction of a few predators.

Finally, we ran numerical simulations for the case of a predator population chasing with a

preference for adults, i.e. $\gamma < 1$. In this case, an oscillatory behaviour in the outer zone is still observed and it is also periodic.

To conclude, due to an absence of preys in the intermediate zone, cats cannot reach the inner zone, so the bird population persists in the inner zone. In the outer zone, a periodic dynamic occurs when the preference coefficient γ takes average values, as in the spatially unstructured model, see previous section.

Three species invasion numerical results

In this series of numerical simulations we consider a model with an introduced prey, given by system (13). Cats and rabbits are invading the spatial domain at time $t=0$ by the subdomain located on the left part of the outer zone. Initial conditions for the native prey populations and the alien predator population are as above, see Figure 4; initial density for the introduced prey is depicted in Figure 7.

First, we process numerical experiments for the predator-2 preys model with two age stages in the prey population and preference of the predator for the juvenile stage, $\gamma=2$. In addition, we consider that cats have a preference coefficient $\alpha=1.5$, for native prey over alien prey.

The rabbit population settles on the intermediate zone. As a consequence, cats can invade intermediate and inner zones, inducing both cat and bird extinction in the inner zone. In addition, after the extinction of the native prey population, an oscillatory behaviour occurs in the outer zone, due to the diffusion of the large alien prey population present in intermediate zone. Next, oscillations appear in the intermediate zone in a similar way than for the bird-cat model with

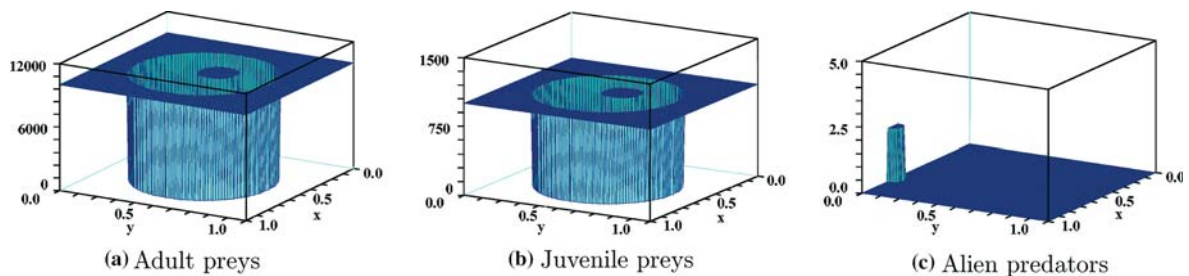


Figure 4. Initial conditions for the age structured model (10).

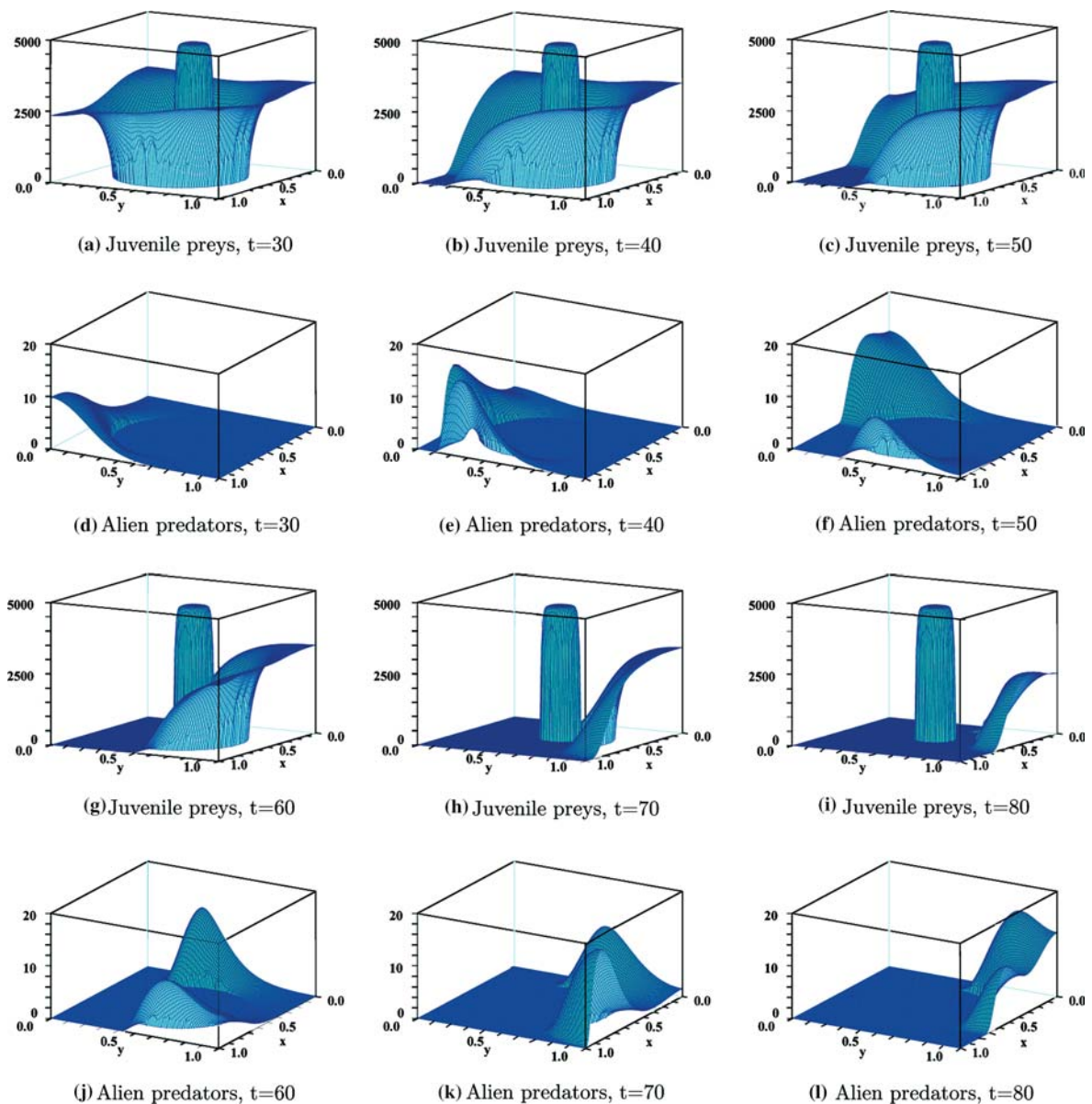


Figure 5. Transient behaviour for the age structured model (10) when cats have a strong preference for juveniles, $\gamma=2$. Note the oscillatory dynamical behaviour.

two age stages for the bird population, see previous subsection. A long time transient behaviour of the system is depicted in Figure 8.

Next we consider a higher growth rate for the alien prey population, i.e. $r_r=1.89$. Numerical experiments show the same extinction dynamic as far as the native prey population is concerned. For alien populations, a different dynamic occurs. After the global extinction of the native preys, we

have coexistence of both introduced populations as an asymptotic behaviour, see Figure 9.

Discussion

In this paper we have presented a spatial model concerning a three species predator-2 preys system. We considered an alien predator population

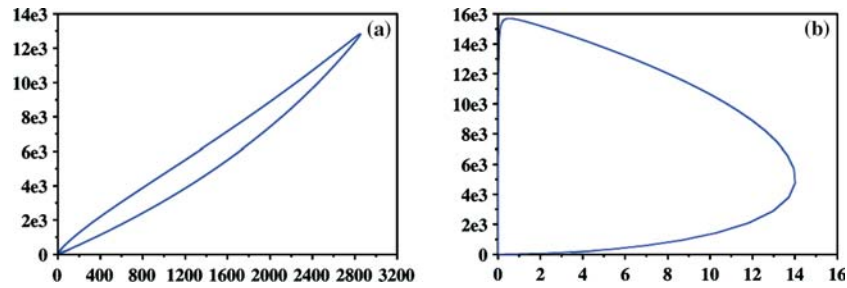


Figure 6. Trajectory at location $(x=0.7, y=0.03)$ of the outer zone for the age structured model (10) in the (A, J) phase plane (a), $(C, P=A+J)$ phase plane (b).

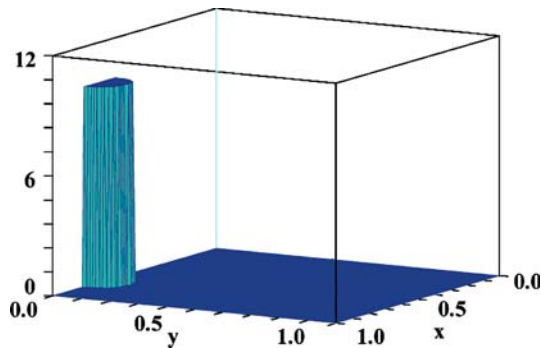


Figure 7. Initial condition for the alien prey in (13).

(cat, *Felis catus* L.) preying both on a native prey species (seabirds) with two age stages, and on an introduced prey (rodents or rabbits). The main feature of these models is the ability to predict the extinction in finite or infinite time of one or more species and the occurrence of time periodic dynamics.

First we considered the case of a native species split into two age stages; in absence of alien predators and alien competitor preys, we presented a condition for the persistence of the native prey

population. For the case of a long-living native prey population, an elasticity analysis points out that natality and maturation rates are the more influential parameters in the model with two age stages. We derived a two species alien predator-native prey system with two age stages for the native prey population. This model can predict several dynamical behaviours, such as extinction in finite or infinite time of one or more species, stable coexistence and, more interestingly, periodic dynamics. A mathematical analysis shows that for average values for the preference, γ , of cats for either juvenile or adult stages, the model yields periodic dynamics. Extreme values of γ yield different dynamics. For a long living species with low fertility, extreme values of γ induce extinction of both alien predator and native prey species, with possible damped oscillations. It is still true when we consider low values for the preference coefficient in a short-lived native prey species with a high fecundity. However, in this last case, for a high preference for the juvenile stage, both populations will coexist in a stable asymptotic persistent state.

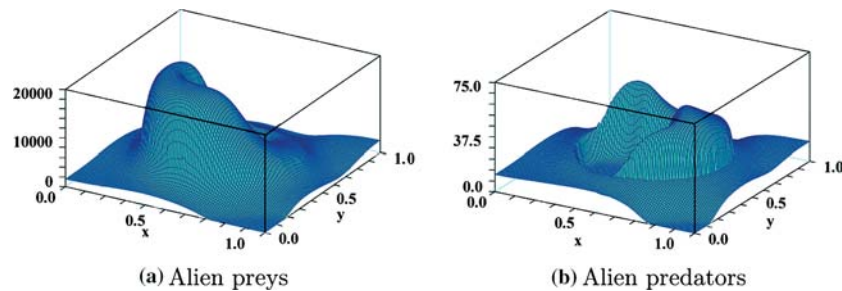


Figure 8. Some results on the long time behaviour of the predator-2 preys system: transient behaviour. Extinction of both populations arises in inner zone, and oscillations appear in intermediate and outer zones.

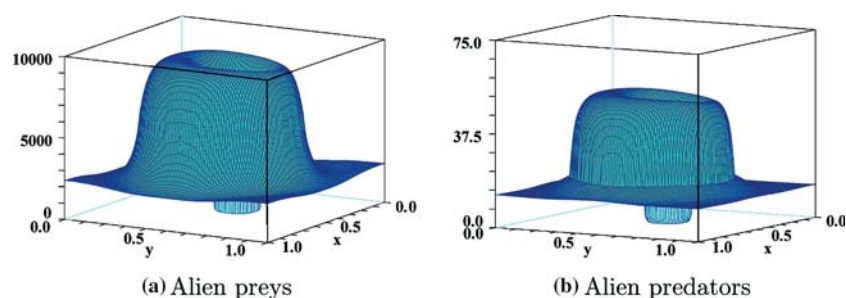


Figure 9. Another scenario for the predator-2 preys system: asymptotic behaviour. Native prey population goes extinct in the whole spatial domain. Alien populations coexist in intermediate and outer zone but cannot survive in the inner zone.

We built spatially dependent versions of the previous models in the spirit of those described in Gaucel and Langlais (2002), Gaucel et al. (2005) leading to reaction-diffusion systems including a further alien introduced prey. Heterogeneity of the spatial domain is depicted by three patches, which can be hospitable or hostile habitats, depending on species. Our idea is to model an isolated oceanic island, e.g., the main island of the Kerguelen Archipelago. We use numerical experiments to point out the main effects of the predator food preference on the dynamic. As a conclusion, the success of cat invasion in the inner zone is strongly dependent on the presence of an introduced prey population to help predators to go through the intermediate zone, which bring to the fore the buffer role played by the introduced prey population in the intermediate zone. In absence of introduced preys, we have analysed the effects of a population of cats preying on juvenile and adult seabirds in a case of long living native species with a low fecundity. One interesting feature is the oscillatory behaviour, which appears in the outer zone for average hunting preference γ . For the predator-2 preys model, the alien prey population, i.e. rabbit population, easily reaches and colonises the intermediate zone so the cat population can invade the intermediate and inner zones; extinction of both species in the inner zone occurs. It is important to note that, for a short-lived seabird species with a high fecundity, we could obtain stable coexistence of both species in the inner zone as an asymptotic state. After the extinction of the native prey population, further dynamic depends on the values of the alien populations growth rates; we observed stable coexistence and periodic dynamic as possible outcomes.

As a conclusion, the numerical study of the model with the native prey population split into two age stages gives more precisely the future of this native species and should help us to protect it.

When an oscillating dynamic is observed, a long period of coexistence of both species could appear, which can induce some misinterpretation of the long term dynamical behaviour. Moreover, population could stay at low values for a long time, so it may be interesting to consider some stochastic effects when population densities become low.

In the future we shall extend this work by taking into account the seasonality of the parameters, for example the duration of the respective reproductive seasons for each species; this approach should give additional numerical results and should help us to determine which will be the more efficient strategy to protect the native species.

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References

- Arditi R and Berryman A-A (1991) The biological control paradox. *Trends in Ecology and Evolution* 6: 32
- Atkinson IAE (1985). The spread of commensal species of *Rattus rattus* to oceanic islands and their effects on islands avifaunas. In: Moors PJ (ed) *Conservation of Island Birds*, Vol 3, pp 35–81. ICPB Technical Publication

- Bloomer J-P and Bester M-N (1990) Diet of a declining feral cat *Felis catus* population on Marion Island. South African Journal of Wildlife Research 20: 1–4
- Bried J and Jouventin P (2002) Site and mate choice in seabirds: an evolutionary approach. In: Schreiber EA and Burger J (eds) Biology of Marine Birds, pp 263–305. CRC Press, Boca Raton, FL
- Cantrell R-S and Cosner C (1993) Should a park be an island? SIAM Journal of Applied Mathematics 53: 219–252
- Cantrell R-S and Cosner C (2003) Spatial Ecology via Reaction-Diffusion Equations. Wiley Series in Mathematical and Computational Biology, Wiley
- Courchamp F and Sugihara G (1999) Modeling the biological control of an alien predator to protect island species from extinction. Ecological Applications 9: 112–123
- Courchamp F, Langlais M and Sugihara G (1999) Control of rabbits to protect island birds from cat predation. Biological Conservation 89: 219–225
- Derenne P (1976) Notes sur la biologie du chat haret de Kerguelen. Mammalia 40: 531–595
- Fagan W-F, Cantrell R-S and Cosner C (1999) How habitat edges change species interactions. The American Naturalist 153: 165–182
- Gaucel S and Langlais M (2002) Some mathematical problems arising in heterogeneous insular ecological models. Revista de la Real Academia de Ciencias Exactas Físicas y Naturales Serie A Matemáticas 96: 389–400
- Gaucel S, Langlais M and Pontier D (2005) Invading introduced species in insular heterogeneous environments. Ecological Modelling (in press)
- Keitt BS, Wilcox C, Tershy BR, Croll DA and Donlan CJ (2002) The effect of feral Cats on the population viability of Black-vented Shearwaters (*Puffinus opisthomelas*) on Navidad Island. Mexico Animal Conservation 5: 217–223
- Lack D (1968) Ecological Adaptations for Breeding in Birds. Methuen, London
- Moors PJ, Atkinson IAE and Sherley GH (1992) Reducing the rat threat to island birds. Bird Conservation International 2: 93–114
- Murray J-D (2002) Mathematical Biology, 3rd edn. Biomathematics Series 19, Springer Verlag, Berlin
- Pontier D, Say L, Debias F, Bried J, Thioulouse J, Micol T and Natoli E (2002) The diet of feral cats (*Felis catus* L.) at five sites on the Grande Terre, Kerguelen archipelago. Polar Biology 25: 833–837
- Shigesada N and Kawasaki K (1997) Biological Invasions: Theory and Practice. Oxford Series in Ecology and Evolution. Oxford University Press, Oxford
- Stattersfield AJ and Capper DR (2000) Threatened Birds of the World. BirdLife International and Lynx Edicions, Barcelona
- Veitch CR (1985) Methods of eradicating feral cats from offshore islands in New Zealand. In: Moors PJ (ed) Conservation of Island Birds. ICBP Technical Publication Vol 3, 125–141
- Weimerskirch H, Clobert J and Jouventin P (1987) Survival in five southern albatrosses and its relationship with their life history. Journal of Animal Ecology 56: 1043–1055
- Weimerskirch H, Zolner R and Jouventin P (1989) The avifauna of the Kerguelen Islands. Emu 89: 15–29