Stabilizing Effect of Prey Competition for Predators Exhibiting Switching Feeding Behavior

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Abstract: The classical model by Tanksy on a two-level food web with a predator feeding on two kinds of prey is revisited and extended. The ecosystem with intraspecific and interspecific competition for resources among the prey is analized. Two equilibria are found: a segment of conditionally (neutrally) stable equilibrium points and the interior coexistence equilibrium, which is proven to be inconditionally stable. The predator population settles to a lower level than the one arising in the original Tansky's model. In addition, there is inverse proportionality between the predators' mortality and the equilibrium value. Predators' recovery and the settling of the system toward coexistence are also allowed by a large prey carrying capacity.

Key–Words: Predator-prey, switching mechanism, Tansky model, competition, stable equilibria

1 Introduction

In mathematical biology population theory plays a fundamental role. Historically indeed, the first model was formulated by the economist Malthus [23], and later on corrected for logistic, i.e. more realistic, behavior by Verhulst [28, 30, 29]. It is well known that modern biomathematics originated from the works of Volterra and Lotka at the beginning of the past century, [22, 33]. The researches were prompted by the unexpected results of fish catches in the Adriatic Sea in the years immediately after World War I, [6]. Since then the subject has grown and nowadays several international Journals are entirely devoted to this topic.

In the original works of Volterra and Lotka, an environment is considered in which two populations interact, and the former, the prey, is the sole food resource for the latter. Such an environment is not so highly unrealistic, as sharks in the ocean feed only on smaller fish, in the absence of which they certainly would starve. For terrestrial and avian populations, the model could be suitably modified to take into account other food sources. Later developments of the theory account for food webs, in which several trophic levels exist and each population is a predator of the one in the lower trophic level and a source of food for the one in the upper one. A top predator dominates the chain, [7, 10]. For recent results on this topic, see for instance [4, 5, 11, 16, 19, 20, 27], were even chaotic behavior and bifurcations can be accounted for in such models. From the ecological viewpoint, food chains may even be related to eutrophycation of marine environments, [2, 3, 21]. Predator-prey models have also been analyzed when their parameters are functions of time, see [8] or the environmental fluctuations are accouted for by allowing stochasticiy to play a role, [9]. More complex models involve the description of the populations by accounting of cohorts, i.e. describing the evolution of subsets of the population in which the individuals share the same birthdate range, modeled via age-dependent densities, or the same range of body size or form, in such case giving more general systems known as stage-dependent model, [35]. Such description has also been extended to the more recent ecoepidemic models, [31], in which an underlying demographic model with interacting species is affected by a disease spreading at least in one of the two populations.

Further elaborations of the basic model involve competition for food among species. A current such example of the former is given by the American grey squirrel which has been imported and released in the European environment. The unwanted consequence is that the former is gradually replacing the autoctonous species. But to biologists and environmentalists many other similar examples in which the exotic species always outperforms the local one are currently known. Also of interest are systems describing symbiotic interactions or commensalism, in which both popula-

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tions benefit from the presence of the other one. Classical examples are the anemone and the damsel fish, the bees pollinating the flowers, but for more recent findings, see [12, 34].

In real ecosystems, where several species are present, predators in general have the possibility of feeding on different prey. This situation has also been analyzed by mathematical models. More refined formulations thus allow for the predators the active selection of the food source. This choice in the classical Tanksy model [26] is based essentially on the relative abundance of the two populations. Further work on this topic has been carried out in the past years, [13, 14, 15]. Tansky's model has been recently modified, [24, 32] to take into account a logistic term. In the context of trophic systems, such an idea has been considered for instance in [17]. Here we introduce a further modification, in which the two prey live on shared resources.

The paper is organized as follows. In the next two Sections we briefly review Tansky's model, [26] and outline some earlier generalizations. In Section 4 we formulate the new model, and establish its equilibria in the following Section. Section 6 contains their stability analysis. The results are discussed in Section 7, providing also some biological and environmental consequences as well as ecological interpretations of the mathematical analysis. A further extension is outlined in the final Section.

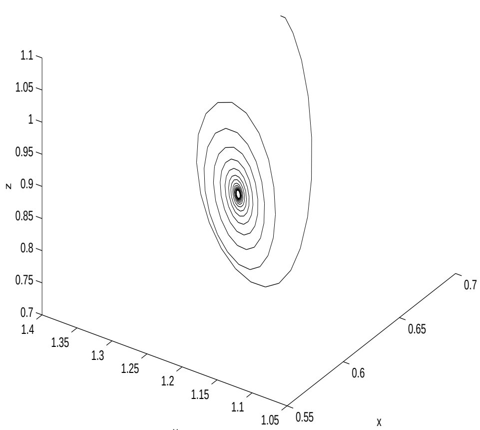

Figure 1: Tanksy's model: stable coexistence equilibrium

2 The Background Model

The classical model for a two-prey and one-predator system in which the latter hunts the type of preferred prey is given by the following system of equations, [26]

$$\frac{dx}{dt} = \left(R_1 - \frac{az}{1+\frac{y}{x}}\right)x = \left(R_1 - \frac{axz}{x+y}\right)x, \qquad (1)$$

$$\frac{dy}{dt} = \left(R_2 - \frac{bz}{1+\frac{x}{y}}\right)y = \left(R_2 - \frac{byz}{x+y}\right)y,$$

$$\frac{dz}{dt} = \left(-R_3 + \frac{ax^2}{x+y} + \frac{by^2}{x+y}\right)z,$$

where respectively x and y are the populations of the two kinds of prey and z denotes the predator species. As for the parameters appearing in the equations, R_1, R_2 and R_3 represent the Malthus' net growth rates of each prey population, and the mortality of the predators respectively. The parameters a and b instead represent the predator's successful hunting rates. All the above parameters are assumed to be nonnegative. The model is constructed essentially from the Lotka-Volterra model, in which the functional response for feeding is assumed to possess a Holling type II, or Michaelis-Menten, form. Such type of modification is due to the assumption that a too abundant type of prey is ignored by the predators, after a successful hunt. For an example of this sort in the literature see [1]. However, the Michaelis-Menten term is modified, to include in the denominator the ratio of the two prey populations, so that depending on which one prevails, the predators will consequently hunt preferably the more abundant species. When one of the prey populations becomes small, the predator switches the predation mainly to the other species. At the same time, the reduced hunting rate on the smaller population allows its individuals to better find hiding places and thus more easily escape from fatal interactions with predators. This fact leads to a possible recovery from the low population values in spite of the predators' hunting efforts.

Specific feature of this model is the possibility of Hopf bifurcations of the interior system's equilibrium, originating limit cycles for the populations involved. We show our simulations for two sets of parameters, one leading to the stable coexistence equilibrium, Figure 1. It is obtained for the parameter values $R_1 = .3$, $R_2 = .6$, $R_3 = 1$, $a = 1$, $b = 1$. The second one instead shows sustained oscillations around it, Figure 2. for the following parameter values $R_1 = .5$, $R_2 = .5$, $R_3 = 1$, $a = 1$, $b = 1$. Clearly the change in the prey reproductive rates and mortality of the predators induces the bifurcation.

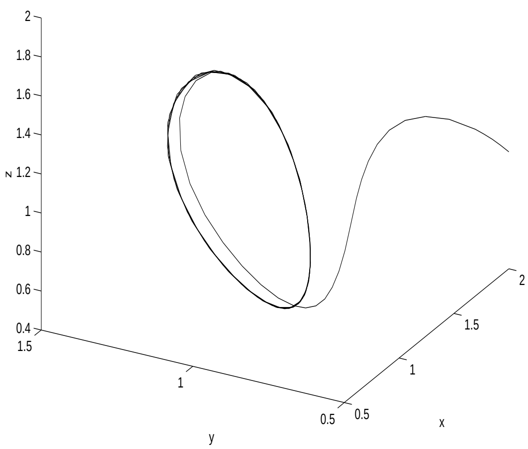

Figure 2: Tanksy's model: limit cycles around the coexistence equilibrium

3 Some Earlier Generalizations

The above model has been reconsidered in [24, 32], by allowing logistic terms in the prey equations with different carrying capacities, K_x and K_y say, thus preventing the unbounded growth of these populations in the absence of predation. Namely, to better render the real life situation, intraspecific population pressures terms of the type

$$\frac{x}{K_x}, \quad \frac{y}{K_y}$$

have been respectively subtracted from the first two equations of (1). These terms contain different carrying capacities because the two prey species are assumed to live on different environments, both accessible by the common predator, but the two prey populations do not exhibit any kind of interaction with each other. We note also that [24] contains another similar model, in which more general response functions $A_j(x_1, x_2)$, $j = 1, 2$ are introduced, here x_j representing the two prey species. But the assumptions on them remain the same, the two prey species live in different habitats never interacting with each other.

4 The New Model

In this study, we will further modify the corrected model to make it even more realistic, by observing that in general the predator is a carnivorous species which usually feeds on herbivores. The latter thus share the same pasture, and therefore compete for this resource. Thus there must be a common carrying capacity K for the environment to support both prey species, and they feel the total population pressure not only of their similar but also of the second species present in the environment. Thus the modification of (1) contains in both prey evolution equations the same cumulative logistic term of the form

$$\frac{x+y}{K},$$

accounting for both intraspecific and interspecific prey interactions.

In view of the above discussion, the system (1) becomes

$$\begin{aligned}
\frac{dx}{dt} &= \left[R_1\left(1-\frac{x+y}{K}\right)-\frac{az}{1+\frac{y}{x}}\right]x, \quad (2)\\
\frac{dy}{dt} &= \left[R_2\left(1-\frac{x+y}{K}\right)-\frac{bz}{1+\frac{x}{y}}\right]y,\\
\frac{dz}{dt} &= \left[-R_3+\frac{ax}{1+\frac{y}{x}}+\frac{by}{1+\frac{x}{y}}\right]z,
\end{aligned}$$

where K denotes the environment's carrying capacity for the two prey species and the other parameters retain their meaning as in (1). Again here the parameters of the model are to be taken as nonnegative real numbers.

5 Equilibrium Points

Observe that all trajectories of (2) are bounded. For this, it suffices to define $\Psi = x + y + z$, $R = \max\{R_1, R_2\}$, $r = \min\{R_1, R_2\}$ and to take a constant $0 < \eta < R_3$. Summing the equations (2), we have the estimates

$$\frac{d\Psi}{dt}+\eta\Psi \le (x+y)\left[(R+\eta)-\frac{r}{K}(x+y)\right]$$
$$-z(R_3-\eta) \le \frac{K(R+\eta)^2}{4r} \le \frac{K(R+R_3)^2}{4r} \equiv L$$

having taken the maximum of the parabola in $x + y$. It follows that

$$\frac{d\Psi}{dt} \le -\eta\Psi + M$$

implies then

$$\Psi(t) \le \frac{M}{\eta} \equiv L \quad (3)$$

for every $t \ge 0$, from which the claim. It makes sense at this point to concentrate the analysis to the ω-limit set, which must be contained in the compact positively invariant set just found, i.e. the portion in the feasible phase space of the ball of radius L centered at the origin, $B_L(O)$.

The equilibria of system (2) are the origin P_a, the following two boundary points

$$P_b = \left(0, \frac{R_3}{b}, \frac{R_2(bK - R_3)}{b^2 K}\right),$$
$$P_c = \left(\frac{R_3}{a}, 0, \frac{R_1(aK - R_3)}{a^2 K}\right),$$

and letting q be an arbitrary nonnegative real parameter, the additional boundary segment of equilibria expressed by $P_d = (K - q, q, 0)$ and finally the interior coexistence equilibrium $P_e = (\tilde{x}, \tilde{y}, \tilde{z})$ with components

$$\begin{aligned}
\tilde{x} &= R_1 R_3 \frac{bR_1 + aR_2}{(R_1^2 b + aR_2^2)a}, \\
\tilde{y} &= R_2 R_3 \frac{bR_1 + aR_2}{(R_1^2 b + aR_2^2)b}, \\
\tilde{z} &= \frac{1}{Kb^2a^2(R_1^2 b + aR_2^2)} \left[KR_1^3 ab^3 - R_1^3 R_3 b^3 \right. \\
&\quad + KR_2 a^2 b^2 R_1^2 + KR_2^3 a^3 b + KR_1 a^2 b^2 R_2^2 \\
&\quad \left. - 3ab^2 R_1^2 R_3 R_2 - 3a^2 b R_1 R_3 R_2^2 - a^3 R_2^3 R_3\right].
\end{aligned} \tag{4}$$

The feasibility conditions for the boundary equilibria are as follows: for P_b we need $bK \geq R_3$, P_c is acceptable if $aK \geq R_3$ and P_d needs the restriction on the otherwise free q parameter, so that $0 \leq q \leq K$.

P_e instead is feasible if and only if

$$K > R_3 \frac{(R_2 a + R_1 b)^2}{ab(R_2^2 a + R_1^2 b)}. \tag{5}$$

6 Stability

We need to address the question whether the equilibria are approached as time flows or system trajectories are instead ultimately repelled away from them. To this end, it is necessary to investigate their stability, which essentially relies on the sign of the eigenvalues of the system's Jacobian at such points. The Jacobian J of (2) is given by

$$\begin{pmatrix}
J_{11} & \frac{ax^2 z}{(x+y)^2} - \frac{R_1 x}{K} & -\frac{ax^2}{x+y} \\
\frac{by^2 z}{(x+y)^2} - \frac{R_2 y}{K} & J_{22} & -\frac{by^2}{x+y} \\
\frac{ax^2+2axy-by^2}{(x+y)^2} z & \frac{by^2+2bxy-ax^2}{(x+y)^2} z & J_{33}
\end{pmatrix} \tag{6}$$

with

$$J_{11} = R_1\left(1 - \frac{2x+y}{K}\right) - \frac{axz(x+2y)}{(x+y)^2},$$
$$J_{22} = R_2\left(1 - \frac{x+2y}{K}\right) - \frac{byz(y+2x)}{(x+y)^2},$$
$$J_{33} = -R_3 + \frac{ax^2 + by^2}{x+y}.$$

The eigenvalues of (6) at the origin are $R_1 > 0$, $R_2 > 0$, $-R_3 < 0$, from which its instability follows.

Similarly at P_b we find the eigenvalues

$$\lambda_1^{(b)} = \frac{R_1(bK - R_3)}{bK}, \quad \lambda_\pm^{(b)} = \frac{-R_2 R_3 \pm \sqrt{\Delta_b}}{2bK}.$$

with

$$\Delta_b = R_2^2 R_3^2 - 4b^2 K^2 R_2 R_3 + 4bKR_2 R_3^2,$$

and in view of the feasibility condition it is immediate to infer that $\lambda_1^{(b)} > 0$, i.e. P_b is also unstable.

For P_c the situation is very similar, as we find the eigenvalues

$$\lambda_1^{(c)} = \frac{R_2(aK - R_3)}{aK}, \quad \lambda_\pm^{(c)} = \frac{-R_1 R_3 \pm \sqrt{\Delta_c}}{2aK}.$$

with

$$\Delta_c = R_1^2 R_3^2 - 4a^2 K^2 R_1 R_3 + 4aKR_1 R_3^2.$$

Once again the feasibility condition implies $\lambda_1^{(c)} > 0$, i.e. P_c is also unstable.

For P_d the eigenvalues are $\lambda_1^{(d)} = 0$ with corresponding eigenvector $\mathbf{w}_1^{(d)} = (1, -1, 0)^T$ and

$$\begin{aligned}
\lambda_2^{(d)} &= \frac{R_1 q - R_1 K - R_2 q}{K}, \\
\lambda_3^{(d)} &= \frac{aK^2 - 2aKq - R_3 K + (a+b)q^2}{K},
\end{aligned}$$

with eigenvectors $\mathbf{w}_3^{(d)} = (0, 0, 1)^T$ and

$$\mathbf{w}_2^{(d)} = \left(R_1\left(1 - \frac{q}{K}\right), R_2 \frac{q}{K}, 0\right)^T.$$

Now $\lambda_1^{(d)} = 0$ gives a kind of neutral stability along the $y = x$ direction, i.e. along the line of equilibria P_d; moreover the feasibility condition $0 \leq q \leq K$ implies that $\lambda_2^{(d)} < 0$. Stability is then governed by the last eigenvalue, namely P_d is (neutrally) stable if

$$aK^2 + (a+b)q^2 < R_3 K + 2aKq, \tag{7}$$

the trajectories in this case approaching the xy phase plane along the vertical z direction.

In order to study the stability of the point P_e we examine the characteristic equation:

$$\lambda^3 + L_1\lambda^2 + L_2\lambda + L_3 = 0, \qquad (8)$$

where, letting

$$A = \frac{\tilde{x}}{\tilde{x}+\tilde{y}}, \quad B = \frac{\tilde{y}}{\tilde{x}+\tilde{y}},$$
$$S_1 = \frac{R_1\tilde{x}}{K}, \quad S_2 = \frac{R_2\tilde{y}}{K},$$

the coefficients are given by

$$\begin{aligned}
L_1 &= bAB\tilde{z} + S_2 + aAB\tilde{z} + S_1;\\
L_2 &= aAB\tilde{z}S_2 + 2\tilde{z}a^2A^2B\tilde{x} + 2b^2B^2\tilde{y}\tilde{z}A\\
&\quad -\tilde{z}\tilde{b}B^2a\tilde{x}A + bS_1AB\tilde{z} - bB\tilde{y}\tilde{z}aA^2\\
&\quad +\tilde{z}a^2A^3\tilde{x} + b^2B^3\tilde{y}\tilde{z} + bB^2\tilde{z}S_1 + S_2aA^2\tilde{z};\\
L_3 &= \tilde{z}^2\tilde{y}abAB[B^3b + aA^3 + aA^2B + AB^2b]\\
&\quad +2\tilde{z}\tilde{y}[-aAB^2bS_1 - S_1bBaA^2 + S_1b^2B^3\\
&\quad +S_1b^2B^2A] + \tilde{z}^2\tilde{x}abAB[bB^3 + bB^2A\\
&\quad +BaA^2 + aA^3] + \tilde{z}\tilde{x}[-2S_2aAbB^2\\
&\quad -2S_2aA^2bB + 2a^2A^2BS_2 + 2S_2a^2A^3].
\end{aligned}$$

Using the Routh-Hurwitz conditions, all eigenvalues have negative real parts if and only if

$$L_1 > 0, \quad L_3 > 0, \quad L_1L_2 - L_3 > 0.$$

In view of its definition, clearly $L_1 > 0$.

Upon substitution of the values of A, B, $\tilde{x}$, $\tilde{y}$, S_1 and S_2, we find that L_1 can be rewritten as a product as follows

$$L_3 \quad = \quad F_1F_2F_3F_4$$

where the quantities on the right are given by

$$\begin{aligned}
F_1 &= \frac{\tilde{z}}{(\tilde{x}+\tilde{y})^2} > 0;\\
F_2 &= \frac{R_3(bR_1 + aR_2)}{a^2b^2K(bR_1^2 + aR_2^2)} > 0;\\
F_3 &= \frac{R_1R_2R_3(bR_1 + aR_2)}{(bR_1^2 + aR_2^2)} > 0;\\
F_4 &= R_2^2a^2bK\tilde{z} + ab^2K\tilde{z}R_1^2 > 0.
\end{aligned}$$

As a consequence it then follows that $L_3 > 0$.

To study the sign of the last quantity, $L_1L_2 - L_3$, let us define

$$\begin{aligned}
f_1 &= a^2b^2zR_1KR_2(f_{1a} + f_{1b});\\
f_2 &= R_3(R_1b + aR_2)^3(f_{2a} + f_{2b});
\end{aligned}$$

and

$$\begin{aligned}
f_{1a} &= 3a^2R_2^2R_1^3b^2 + 3aR_2^2R_1^3b^3 + a^4R_1R_2^4\\
&\quad +aR_2R_1^4b^3 + a^3R_2^4R_1b + 3a^3R_2^3R_1^2b\\
&\quad +R_2R_1^4b^4 + 3a^2R_2^3R_1^2b^2;\\
f_{1b} &= a^2b^2K(R_1 - R_2)^2(R_1^2b + 2R_1bR_2\\
&\quad +2aR_2R_1 + aR_2^2);\\
f_{2a} &= 3R_1^2a^2R_2^3b + R_1a^3R_2^4 + R_1^4b^3R_2\\
&\quad +3R_1^3b^2R_2^2a;\\
f_{2b} &= baK\left[2baR_1^3R_2 + 2baR_2^3R_1\right.\\
&\quad \left.+(R_1^2b - aR_2^2)^2\right];
\end{aligned}$$

so that it follows

$$L_1L_2 - L_3 = \frac{R_3z(f_1 + f_2)}{abK^2(R_1b + aR_2)^4(R_1^2b + aR_2^2)}.$$

Now since $f_{1a} > 0$, $f_{1b} > 0$, $f_{2a} > 0$, $f_{2b} > 0$, we have also $f_1 > 0$ and $f_2 > 0$, from which $L_1L_2 - L_3 > 0$ and thus whenever feasible P_e is inconditionally stable. Notice also that the vanishing of $L_1L_2 - L_3$ would be necessary for getting purely imaginary eigenvalues, so that our result prevents the occurrence of a Hopf bifurcation.

7 Discussion

We have found that among the possible feasible equilibria of the proposed model, only two can be stable, the segment of equilibria P_d, at every point of which the system shows a kind of conditional neutral stability, and the interior coexistence equilibrium P_e. In the former, the predators vanish, and the prey settle to values respectively of $K - q$ and q, with $0 \leq q \leq K$. This can be interpreted as a positive feature in case the predators represent a nuisance for the ecosystem, or instead as a flaw in terms of biodiversity, as the environment with their disappearance becomes poorer. Moreover the proportions of the two prey populations at equilibrium are left essentially undetermined by the model, as the free parameter q does not really set either of them at a specific value. In addition observe that for instance a large carrying capacity K combined with a value of q near 0, and a low predators' mortality rate R_3 make condition (7) not satisfied, so that the only possible equilibrium in such case would be the coexistence one P_e. Since in such case P_e is the only existing locally asymptotically stable equilibrium of the system, and all system's trajectories must enter the positively invariant set $B_L(O)$, P_e attracts thus all trajectories originating in the positive phase space, making it a global attractor for the dynamical system. This result is somewhat intuitive, since one would expect that the low mortality rate would enhance the predators survival. In this environment instead the presence of the two prey species helps the predators to recover, even if their birth rates fall to very low levels.

Notice also that in the original Tansky model the internal equilibrium point is $P_T = (x_T, y_T, z_t)$ with equilibrium population values given by

$$x_T = \frac{R_1 R_3 (R_1 b + R_2 a)}{a(R_1^2 b + R_2^2 a)}, \quad (9)$$
$$y_T = \frac{R_2 R_3 (R_1 b + R_2 a)}{b(R_1^2 b + R_2^2 a)},$$
$$z_T = \frac{R_2}{b} + \frac{R_1}{a}.$$

and in the proposed model it is given by (4). Thus the two prey populations at equilibrium are at the very same level in both models. This in spite of the fact that apparently, in the model formulation, they are made to compete with each other for living resources. The necessary disappearance of one of the competitors, namely the principle of exclusion, is in this case violated, due to the presence of the predators in the environment. On the other hand, the predators' level instead is different in the two formulations, specifically it settles to a lower level in our formulation, namely

$$\tilde{z} = \frac{R_2}{b} + \frac{R_1}{a} - \frac{R_3(R_1 b + aR_2)^3}{Kb^2 a^2 (R_1^2 b + aR_2^2)}.$$

The introduction of logistic growth and interspecific competition for the prey has thus the effect of lowering the equilibrium level of the predators.

From the value of $\tilde{z}$, notice further that the amount by which the predators' level z_T in (4) is decreased depends on the carrying capacity K of the prey species. More specifically, the larger prey population the environment is able to to support, the closer to $\tilde{z}$ the predators level will result. On the other hand, the higher the predators' mortality is, the farther the predators' equilibrium value $\tilde{z}$ in the proposed model will be from the original reference value z_T, as expected. Again this is a kind of intuitive result.

Finally, observe that the interior equilibrium P_e is inconditionally stable. This is a similar result as obtained in [24, 32], where in fact, it is shown that the switching feeding behavior makes limit cycles present in the model without the diet disappear. For that purpose, the latter are modeled via a Michaelis-Menten type feeding responses, a more general function than the quadratic one considered here. In spite of this, the stability of the coexistence population levels appears then to be independent of the particular functional response chosen to model the predation process. In the context of food webs, stabilization due to external factors can occur, [18]. The predators' level in the coexistence equilibrium P_e is driven to zero by higher intrinsic mortality rates R_3 or lower prey carrying capacities K, along the vertical direction, $\mathbf{w}_3$. When predators vanish, P_e hits the xy coordinate plane, and there it moves along the eigendirections $\mathbf{w}_2$, until they hit a point on the line $y = x$, thus toward one of the only possible equilibria P_d.

8 The Extended Model

We allow here the system to encompass a more general situation, namely when the prey have different habitats that overlap in part. In such case thus they would share for instance only a common pasture, but have available other food resources somewhere else, inaccessible by the other prey species. Competition in this case must be weighted, meaning that the prey may overlap their feeding territories only partially. Letting the parameters attain once again only nonnegative values, we have

$$\frac{dx}{dt} = \left[R_1\left(1 - \frac{\alpha x + \beta y}{K}\right) - \frac{az}{1 + \frac{y}{x}}\right]x,$$
$$\frac{dy}{dt} = \left[R_2\left(1 - \frac{\alpha x + \beta y}{K}\right) - \frac{bz}{1 + \frac{x}{y}}\right]y,$$
$$\frac{dz}{dt} = \left[-R_3 + \frac{ax}{1 + \frac{y}{x}} + \frac{by}{1 + \frac{x}{y}}\right]z, \quad (10)$$

We expect the former equilibria to be particular cases of the ones of this system. In fact we find among the equilibria again the origin $E_a \equiv P_a$, and the neutrally stable line $E_d \equiv ((K - \beta q)/\alpha, q, 0)$, and the two boundary points

$$E_a \equiv \left(0, \frac{1}{b}R_3, \frac{R_2}{b^2 K}(bK - \beta R_3)\right),$$
$$E_b \equiv \left(\frac{1}{a}R_3, 0, \frac{R_1}{a^2 K}(aK - \alpha R_3)\right).$$

Further, the interior coexistence equilibrium is given in this case by the point $E_e \equiv (\widehat{x}, \widehat{y}, \widehat{z})$ with

$$\widehat{x} \equiv \frac{1}{a}R_1 R_3 \frac{R_1 b + aR_2}{R_1^2 b + aR_2^2}, \widehat{y} \equiv \frac{1}{b}R_3 R_2 \frac{R_1 b + aR_2}{R_1^2 b + aR_2^2},$$
$$\widehat{z} = \frac{1}{Kb^2 a^2 (R_1^2 b + aR_2^2)}(KR_1^3 ab^3 + KR_1 a^2 b^2 R_2^2$$
$$+KR_2 a^2 b^2 R_1^2 + KR_2^3 a^3 b - R_1^3 \alpha R_3 b^3$$
$$-2R_1^2 \alpha R_3 b^2 a R_2 - R_1 \alpha R_3 b a^2 R_2^2$$
$$-aR_2 \beta R_3 R_1^2 b^2 - 2a^2 R_2^2 \beta R_3 R_1 b - a^3 R_2^3 \beta R_3$$

Note that the boundedness result of Section 5 still holds for the trajectories of this system, as we need only to define

$$R = \max\left\{\frac{R_1 + R_3}{\alpha}, \frac{R_2 + R_3}{\beta}\right\}$$

and

$$r = \min\left\{\frac{R_1}{\alpha}, \frac{R_2}{\beta}\right\}$$

to find for $0 \le \eta \le R_3$ the estimate

$$\begin{aligned}\frac{d\Psi}{dt} + \eta\Psi \le \frac{R_1 + R_3}{\alpha}\alpha x + \frac{R_2 + R_3}{\beta}\beta y \\ -\frac{1}{K}(\alpha x + \beta y)\left(\frac{R_1}{\alpha}\alpha x + \frac{R_2}{\beta}\beta y\right) \\ \le R(\alpha x + \beta y) - \frac{r}{K}(\alpha x + \beta y)^2 \le \frac{KR^2}{4r} \equiv \widehat{L}\end{aligned}$$

having taken the maximum of the parabola in $\alpha x + \beta y$ in this context. The conclusion of the proof is as before.

The Jacobian $\widehat{J}$ of (10) is given by

$$\begin{pmatrix} \widehat{J}_{11} & \frac{ax^2z}{(x+y)^2} - \frac{\beta R_1 x}{K} & -\frac{ax^2}{x+y} \\ \frac{by^2z}{(x+y)^2} - \frac{\beta R_2 y}{K} & \widehat{J}_{22} & -\frac{by^2}{x+y} \\ \frac{ax^2+2axy-by^2}{(x+y)^2}z & \frac{by^2+2bxy-ax^2}{(x+y)^2}z & \widehat{J}_{33} \end{pmatrix} \quad (11)$$

with

$$\begin{aligned}\widehat{J}_{11} = R_1\left(1 - \frac{\alpha x + \beta y}{K}\right) - \frac{\alpha R_1 x}{K} \\ -2\frac{axz}{x+y} + \frac{ax^2z}{(x+y)^2}, \\ \widehat{J}_{22} = R_2\left(1 - \frac{\alpha x + \beta y}{K}\right) - \frac{\beta R_2 y}{K} \\ -2\frac{byz}{x+y} + \frac{by^2z}{(x+y)^2}, \\ \widehat{J}_{33} = -R_3 + \frac{ax^2 + by^2}{x+y}.\end{aligned}$$

Rather than proceeding with the extension of the previous analysis to this generalized system and as a validation of the theoretical results formerly obtained, we turn to simulations of the solutions behavior. We consider even a further generalization where the competition terms are different for each species, namely we distinguish the intraspecific competition rate ϕ for the prey x, the corresponding one ψ for the prey y, the interspecific ocmpetition rate of prey y onto prey x, γ, and the corresponding one for the prey x onto prey y, δ. The new equations then read

$$\begin{aligned}\frac{dx}{dt} &= \left[R_1\left(1 - \frac{\phi x + \gamma y}{K}\right) - \frac{az}{1 + \frac{y}{x}}\right]x, \\ \frac{dy}{dt} &= \left[R_2\left(1 - \frac{\delta x + \psi y}{K}\right) - \frac{bz}{1 + \frac{x}{y}}\right]y, \\ \frac{dz}{dt} &= \left[-R_3 + \frac{ax}{1 + \frac{y}{x}} + \frac{by}{1 + \frac{x}{y}}\right]z, \qquad (12)\end{aligned}$$

In Figure 3 we compare the three populations as functions of time obtained integrating the Tansky's model on the left and the generalized extended model on the right. The parameter values of the former as in Figure 1, namely $R_1 = .3$, $R_2 = .6$, $R_3 = 1$, $a = 1$, $b = 1$. The right column instead contains for the same parameter values the integration of model (12), with the remaining parameters given by $K = 100$, $\phi = 0.48$, $\psi = 0.82$, $\gamma = 0.37$, $\delta = 0.42$. Evidently in this case both (1) and (12) behave similarly.

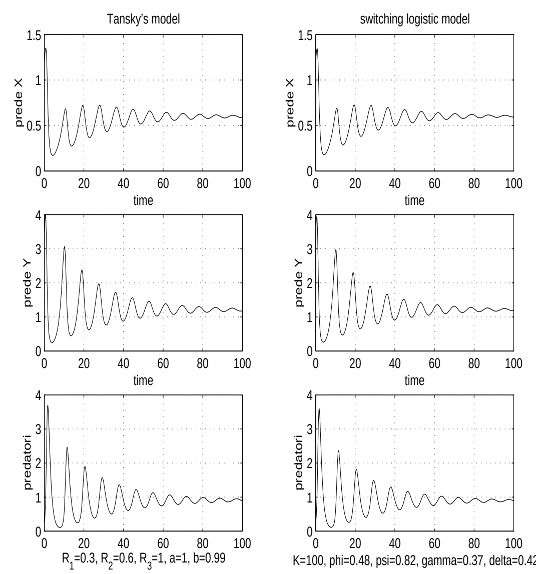

Figure 3: Comparison of time series solutions of Tanksy's model (left) with generalized extended model (right): stable coexistence equilibrium in both cases

Figure 4 instead shows the analogous of Figure 2 for the same parameter values of Tansky's model, namely $R_1 = .5$, $R_2 = .5$, $R_3 = 1$, $a = 1$, $b = 1$, with the corresponding behavior of (12), for the extra parameter values given as above, $K = 100$, $\phi = 0.48$, $\psi = 0.82$, $\gamma = 0.37$, $\delta = 0.42$.

In this case there are also oscillations in the more general model, but it is not clear whether they are sustained or not. To investigate this point, we increased

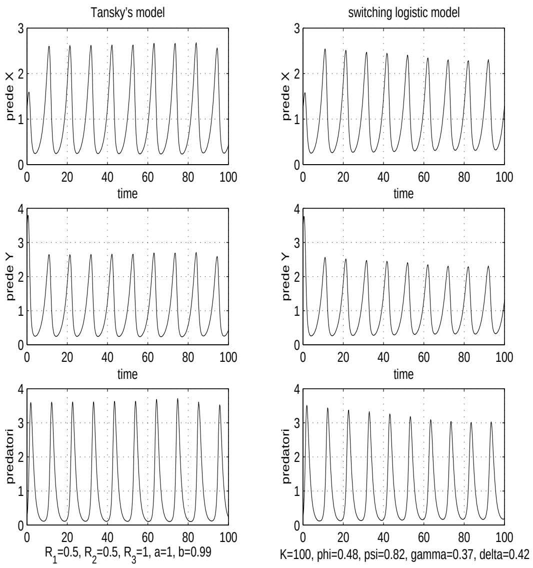

Figure 4: Comparison of time series solutions of Tanksy's model (left) with generalized extended model (right): limit cycle for the former, apparent limit cycles for the latter

the length of the integration interval, thereby obtaining the results reported in Figure 5. It is apparent that the oscillations are not sustained. This result supports the theoretical claim that the interior equilibrium of the generalized model is unconditonally stable, as we have been shown for (2).

To analyze the behavior of unstable equilibria, we integrate the system giving one set of initial conditions lying on the equilibrium and other ones at nearby points, and plot the resulting solutions. We have chosen parameter values so that the equilibria of (2) can be investigated, since for the latter the initial conditions can be analytically given on the system's equilibria. Specifically, we take $R_1 = 0.5$, $R_2 = 0.5$, $R_3 = 1.0$, $a = 1.0$, $b = 0.99$, $K = 100$, $\alpha = 0.48$, $\beta = 0.82$, $\phi = \alpha$, $\psi = \beta$, $\gamma = \beta$, $\delta = \alpha$, $q = 0.3$. The starred solutions are those with such initial conditions. The perturbed solutions, continuous lines, have initial conditions perturbed by an additional positive amount $\epsilon = +0.001$ in all Figures 6-8. Note that in Figure 6 the the solution at the equilibrium has the x population which remains at zero level, while the perturbed solution, with an extremely small initial x population, diverges from the equilibrium, so that it seems a contradiction, but it is only an apparent one, since in the second case the x population seems to rise from zero.

Figure 7 shows the behavior of trajectories near E_a, which tend toward the interior coexistence equilibrium.

In Figure 8 a similar behavior occurs, namely the perturbed trajectories near E_b tend again toward the

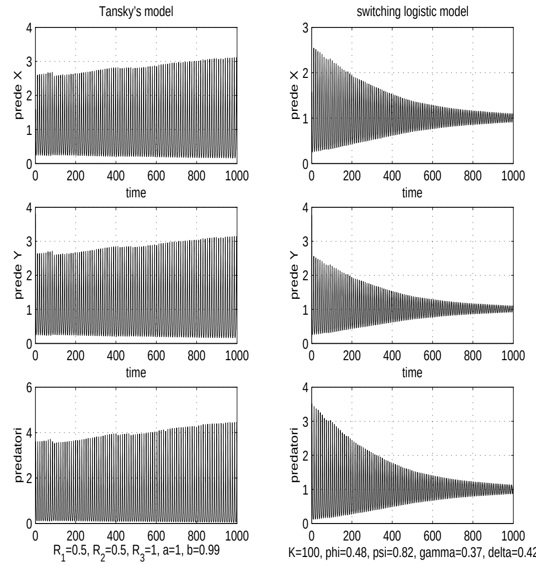

Figure 5: Comparison of time series solutions of Tanksy's model (left) with generalized extended model (right), for longer simulation time: limit cycle for the former, stable coexistence equilibrium for the latter

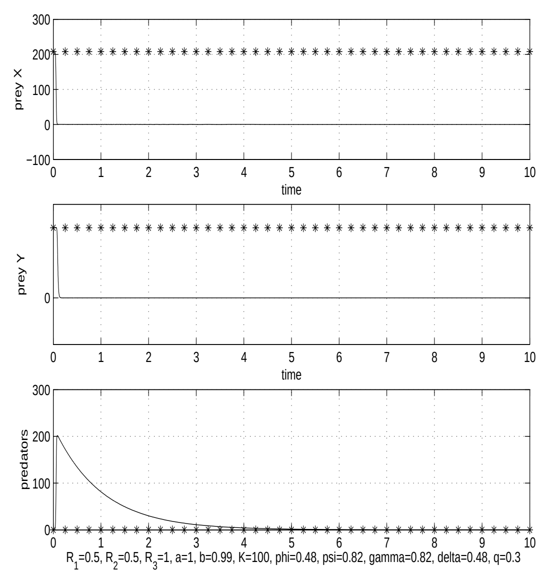

Figure 6: Solution behavior near equilibrium E_d. Notice that the solution at the equilibrium has the x population which remains at zero level, while the perturbed solution, with an extremely small x population, diverges from the equilibrium

interior coexistence equilibrium.

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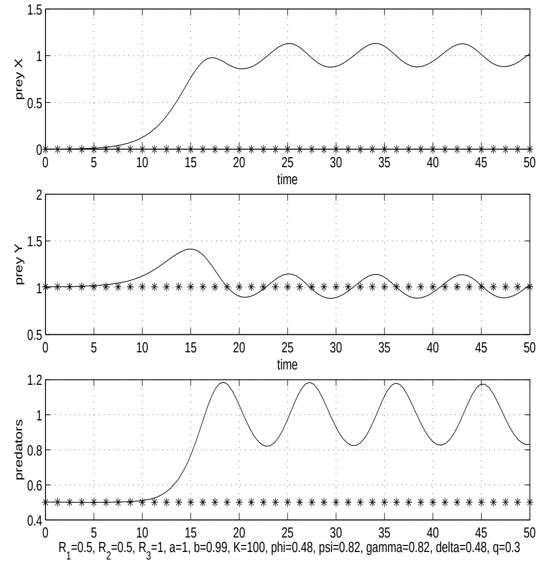

Figure 7: Solution behavior near equilibrium E_a. The perturbed trajectories tend toward the interior coexistence equilibrium

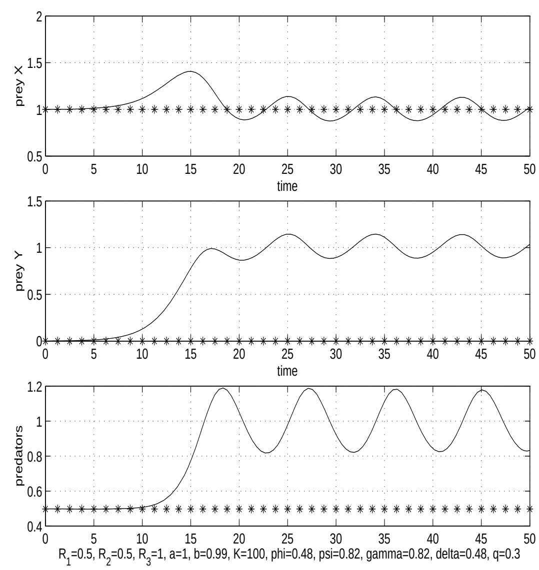

Figure 8: Solution behavior near equilibrium E_b. The perturbed trajectories tend toward the interior coexistence equilibrium

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