A Model of Switching Feeding Behavior for Predators with Prey Inter-species Competition

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Abstract: A mathematical model of a two-prey and one-predator ecosystem with competition for resources among the prey is analyzed. Only a segment of conditionally (neutrally) stable equilibrium points are found together with the interior coexistence equilibrium, which is proven to be inconditionally stable. The latter shows that the predator population settles to a level which is lower than the one obtained from the original Tansky’s model, the lower equilibrium value the higher the predators’ mortality. The latter combined also with a large prey carrying capacity allow the predators’ recovery and the settling of the system toward coexistence.

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 [21], and later on corrected for logistic, i.e. more realistic, behavior by Verhulst [24, 26, 25]. It is well known that modern biomathematics originated from the works of Volterra and Lotka at the beginning of the past century, [20, 28]. 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, 8]. For recent results on this topic, see for instance [4, 5, 9, 14, 17, 18], were even chaotic behavior and bifurcations can be accounted for in such models. From the ecological viewpoint, food chains may even be related to eutrophication of marine environments, [2, 3, 19].

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 autochtonous 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 populations 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 [10, 29].

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 Tansky model [23] is based essentially on the relative abundance of the two populations. Further work on this topic has been carried out in the past years, [11, 12, 13]. Tansky’s model has been recently modified, [22, 27] to take into account a logistic term. In the context of trophic systems, such an idea has been considered for instance in [15]. Here we introduce...
a further modification, in which the two prey live on shared resources.

The paper is organized as follows. In the next Section we briefly review Tansky’s model, [23]. In Section 3 we formulate the new model, and establish its equilibria in the following Section. Section 5 contains their stability analysis. The results are discussed in Section 6, providing also some biological and environmental consequences as well as ecological interpretations of the mathematical analysis.

2 Some Antefacts

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, [23]

\[
\begin{align*}
\frac{dx}{dt} &= (R_1 - \frac{ax}{1 + \frac{y}{x}})x = (R_1 - \frac{axz}{x + y})x, \\
\frac{dy}{dt} &= (R_2 - \frac{bz}{1 + \frac{x}{y}})y = (R_2 - \frac{byz}{x + y})y, \\
\frac{dz}{dt} &= \left( -R_3 + \frac{ax^2}{x + y} + \frac{by^2}{x + y} \right)z,
\end{align*}
\]

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. 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.

The above model has been reconsidered in [22, 27], 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 [22] 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.

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.

3 The new model

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

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

where \(K\) denotes the environment’s carrying capacity for the two prey species and the other parameters retain their meaning as in (1).
4 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

\[
\frac{d\Psi}{dt} + \eta \Psi \leq (x + y) \left[ (R + \eta) - \frac{r}{K}(x + y) \right]
\]

\[
-\varepsilon (R_3 - \eta) \leq \frac{K(R + \eta)^2}{4r} \leq \frac{K(R + R_3)^2}{4r} \equiv L
\]

having taken the maximum of the parabola in \( x + y \). It follows that

\[
\frac{d\Psi}{dt} \leq -\eta \Psi + M
\]

implies then

\[
\Psi(t) \leq \frac{M}{\eta} \equiv L
\]

for every \( t \geq 0 \), from which the claim. It makes sense at this point to concentrate the analysis to the \( \omega \)-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

\[
P_b = \left( 0, \frac{R_3}{b}, \frac{R_2(bK - R_3)}{b^2K} \right),
\]

\[
P_c = \left( \frac{R_3}{a}, 0, \frac{R_1(aK - R_3)}{a^2K} \right),
\]

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

\[
\bar{x} = R_1 R_3 \frac{bR_1 + aR_2}{(R_1^2 b + a R_2^2)a},
\]

\[
\bar{y} = R_2 R_3 \frac{bR_1 + a R_2}{(R_1^2 b + a R_2^2)b},
\]

\[
\bar{z} = \frac{1}{Kb^2 a^2 (R_1^2 b + a R_2^2)} \left[ KR_1^3 ab^3 - R_3^3 R_1 b^3
+ KR_2 a^2 b R_1^3 + KR_3^3 a^2 b + KR_1 a^2 b R_2^3
- 3ab^2 R_1^3 R_3 - 3a^2 b R_1 R_3 R_2^2 - a^3 R_2^3 R_3 \right].
\]

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 \( 0 \leq q \leq K \).

\( P_c \) instead is feasible if and only if

\[
K > \frac{R_3 (R_2 a + R_1 b)^2}{ab (R_2^2 a + R_1^2 b)}.
\]

5 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 system’s eigenvalues at such points. The Jacobian \( J \) of (2) is given by

\[
\begin{pmatrix}
J_{11} & \frac{a x z}{(x+y)^2} - \frac{R_1 x}{K} & -\frac{a x^2}{x+y} \\
\frac{b y^2 z}{(x+y)^2} - \frac{R_2 y}{K} & J_{22} & -\frac{b y^2}{x+y} \\
\frac{a x^2 + 2 a x y - b y^2}{(x+y)^2} & \frac{b y^2 + 2 b x y - a x^2}{(x+y)^2} & J_{33}
\end{pmatrix}
\]

with

\[
J_{11} = R_1 (1 - \frac{2x+y}{K}) - \frac{a x z (x+2y)}{(x+y)^2},
\]

\[
J_{22} = R_2 (1 - \frac{x+2y}{K}) - \frac{b y z (y+2x)}{(x+y)^2},
\]

\[
J_{33} = -R_3 + \frac{a x^2 + b y^2}{x+y}.
\]

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

\[
\lambda^{(b)}_1 = \frac{R_1 (bK - R_3)}{bK}, \quad \lambda^{(b)}_\pm = -\frac{R_2 R_3 \pm \sqrt{\Delta_b}}{2bK},
\]

with

\[
\Delta_b = R_2^2 R_3^2 - 4b^2 K^2 R_2 R_3 + 4b K R_2 R_3^2,
\]

and in view of the feasibility condition it is immediate to infer that \( \lambda^{(b)}_1 > 0 \), i.e. \( P_b \) is also unstable.

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

\[
\lambda^{(c)}_1 = \frac{R_2 (aK - R_3)}{aK}, \quad \lambda^{(c)}_\pm = -\frac{R_1 R_3 \pm \sqrt{\Delta_c}}{2aK},
\]

with

\[
\Delta_c = R_1^2 R_3^2 - 4a^2 K^2 R_1 R_3 + 4a K R_1 R_3^2.
\]

Once again the feasibility condition implies \( \lambda^{(c)}_1 > 0 \), 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

$$
\lambda_2^{(d)} = \frac{R_1q - R_1K - R_2q}{K},
\lambda_3^{(d)} = \frac{aK^2 - 2aKq - R_3K + (a + b)q^2}{K},
$$

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

$$
aK^2 + (a + b)q^2 < R_3K + 2aKq,
$$

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:

$$
\lambda^3 + L_1\lambda^2 + L_2\lambda + L_3 = 0,
$$

where, letting

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

the coefficients are given by

$$
L_1 = bAB\bar{z} + S_2 + aAB\bar{z} + S_1;
L_2 = abAB\bar{z}S_2 + 2\bar{z}a^2A^2B\bar{x} + 2b^2B^2\bar{y}\bar{z}A
- \bar{z}bB^2a\bar{x}A + bS_1AB\bar{z} - bB\bar{y}\bar{z}aA^2
+ \bar{z}a^2A^2\bar{x} + \bar{z}b^2B^3\bar{y}\bar{z} + bB^2\bar{z}S_1 + S_2aA^2\bar{z};
L_3 = \bar{z}^2\bar{y}abAB[B^3b + aA^3 + aA^2B + AB^2b]
+ 2\bar{z}\bar{y}[aAB^2S_1 - S_1B\bar{a}A^2 + S_1b^2B^3
+ S_1b^2B^2A] + \bar{z}^2\bar{y}abAB[bB^3 + bB^2A
+ BaA^2 + aA^3 + \bar{z}\bar{z}[2S_2aAbB^2
- 2S_2aAbB^2 + 2a^2A^2BS_2 + 2S_2aA^2A^3].
$$

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 $A, B, \bar{x}, \bar{y}, S_1$ and $S_2$, we find that $L_1$ can be rewritten as a product as follows

$$
L_1 = F_1F_2F_3F_4
$$

where the quantities on the right are given by

$$
F_1 = \frac{\bar{z}}{\bar{x} + \bar{y}}^2 > 0;
F_2 = \frac{R_3(bR_1 + aR_2)}{a^2b^2K(bR_1^2 + aR_2^2)} > 0;
F_3 = \frac{R_1R_2R_3(bR_1 + aR_2)}{(bR_1^2 + aR_2^2)} > 0;
F_4 = R_2a^2bK\bar{z} + ab^2K\bar{z}R_1^2 > 0.
$$

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

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

and

$$
f_{1a} = 3aR_2R_3^3b^2 + 3aR_2^2R_3^3b^3 + a^4R_1R_2^4
+ aR_2R_1^2b + aR_3^3R_2^2b + R_2R_1R_3^2b^4 + 3a^2R_2^3b^2;
$$

$$
f_{1b} = a^2b^2K(R_1 - R_2)^2R_1^2b^2 + 2R_1bR_2
+ 2aR_2R_1 + aR_2^2;
$$

$$
f_{2a} = 3R_1^2a^2R_2^3b + R_1a^3R_1^2 + R_1^4b^3R_2
+ 3R_3^3bR_2a;
$$

$$
f_{2b} = baK\left[2baR_1^2R_2 + 2baR_1^3R_1
+ (R_1^2b - aR_2^2)^2\right];
$$

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 unconditionally 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.

6 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 $B_t(O), P_e$ 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

$$
\begin{align*}
x_T &= \frac{R_1 R_2(R_1 b + R_2 a)}{a(R_1^2 b + R_2^2 a)}, \\
y_T &= \frac{R_2 R_3(R_1 b + R_2 a)}{b(R_1^2 b + R_2^2 a)}, \\
z_T &= \frac{R_2}{b} + \frac{R_1}{a}.
\end{align*}
$$

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

$$
\bar{z} = \frac{R_2}{b} + \frac{R_1}{a} - \frac{R_3(R_1b + aR_2)^3}{Kb^2a^2(R_1^2b + aR_2^2)}.
$$

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 $\bar{z}$, 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 $\bar{z}$ the predators level will result. On the other hand, the higher the predators’ mortality is, the farther the predators’ equilibrium value $\bar{z}$ 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 [22, 27], 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, [16]. 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, $w_3$. When predators vanish, $P_e$ hits the $xy$ coordinate plane, and there it moves along the eigendirections $w_2$, until they hit a point on the line $y = x$, thus toward one of the only possible equilibria $P_d$.

References:


