

# Introducing A Scavenger Onto A Predator Prey Model\*

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## Abstract

We investigate a generalization of the Lotka-Volterra equations to a three species food chain. This simplified model yields a more complicated dynamical system than models involving logistic-type equations and lends itself to a study or discussion in a modeling of differential equations course.

## 1 Introduction

The important role that scavengers play in ecosystems has long been recognized. In 1877, American naturalist Sanborn Tenney enjoined his colleagues to devote more study to scavengers [11]. Professor Tenney would be disappointed to learn that scavengers have been neglected in population ecology, relative to herbivores and predators. In recent years, the field of systems ecology has placed greater emphasis on the study of detritivores (waste feeders) versus carrion feeding scavengers.

Several mathematical models have been developed to model detritivores [7, 14, 1, 8, 9]. These models all treat the amount of detritus as a distinct state variable. In this paper, we introduce a scavenger into a predator-prey system. We avoid introducing detritus as a variable. The resulting model is simple enough to use analytical techniques to completely characterize the dynamics and serves as a baseline for more complicated interactions. Second, we introduce this model with carrion feeders in mind (e.g. hyenas, vultures, ravens), as the cubic interaction fits naturally to a scavenger versus a detritivore.

A recent review [3] indicates that carrion utilization by terrestrial vertebrates is much more prevalent than previously thought; furthermore, the authors state that terrestrial scavenging has been underestimated by the ecological community. The models of Stephen Heard have been applied to scavenger situations (see [5] for a sample), but, again, these models view resources as an explicit state variable, increasing the dimension of the system. A variety of species specific studies of scavenger and detritivore populations have been conducted. A thorough listing can be found in [5]. We list

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three samples here: In [10], the impact of fishery discards on benthic scavengers is studied, in [6], the impact of elk carrion on large carnivore populations is studied, and in [13], a model of wolf-elk populations that addresses the amount of carrion available to scavengers is developed.

In this paper, we study a three species system, a predator, its prey and a scavenger. The model that we propose is intended to be a baseline model for further investigations. In it, the scavenger species has no impact on the predator or its prey. While this assumption simplifies our analysis, one can envision biological cases when this may occur. As an example, consider the standard hare/lynx system with the introduction of a carrion beetle. It is a reasonable assumption that presence of the beetle neither benefits or inhibits the hare or lynx. We hope to use this model as a first step in understanding scenarios where the scavenger has competitive (or other) effects upon the other species.

## 2 Models upon which we will introduce a scavenger

In this section, we briefly recap some results from the classic Lotka-Volterra predator-prey model [2] upon which we will introduce a scavenger species. The model consists of the following differential equations:

$$\begin{cases} \frac{dx}{dt} = ax - bxy, \\ \frac{dy}{dt} = -cy + dxy, \end{cases} \quad (1)$$

where  $y(t)$  and  $x(t)$  represent, respectively, the predator population and the prey population as functions of time. The parameters  $a, b, c, d > 0$  are interpreted as follows:

- $a$  represents the natural growth rate of the prey in the absence of predators,
- $b$  represents the effect of predation on the prey,
- $c$  represents the natural death rate of the predator in the absence of prey,
- $d$  represents the efficiency and propagation rate of the predator in the presence of prey.

After three changes of variables, we can assume without loss of generality that  $a = 1, b = 1$ , and  $d = 1$  making the system,

$$\begin{cases} \frac{dx}{dt} = x - xy, \\ \frac{dy}{dt} = -cy + xy, \end{cases}, \quad (2)$$

where  $c$  is possibly a different constant than the original system (1). The dynamics of the two systems, before and after the coordinate changes, are identical. With the exception of the fixed point  $(c, 1)$ , all trajectories in positive space are closed curves which are given by the family of equations

$$\ln y - y + c \ln x - x = C,$$

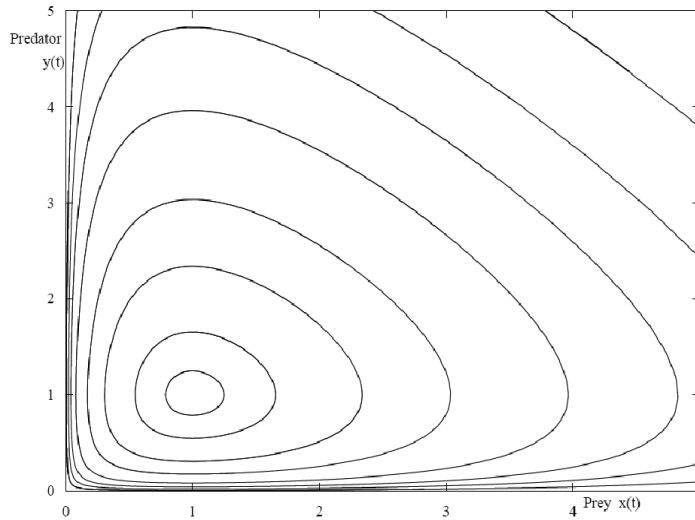


Figure 1: Trajectories of system (2).

where  $C$  corresponds to initial conditions. See Figure 1.

In [12], Volterra himself showed that in any Lotka-Volterra system which has a positive equilibrium, the time averages of the coordinates limit to the values of the equilibrium. In other words, we have,

$$\lim_{T \rightarrow \infty} \frac{1}{T} \int_0^T x(t) dt = c$$

and

$$\lim_{T \rightarrow \infty} \frac{1}{T} \int_0^T y(t) dt = 1$$

where  $(c, 1)$  is the positive equilibrium.

The following can be found in [4], but we include its proof as it is instructive.

LEMMA 2.1 For system (2), we have

$$\lim_{T \rightarrow \infty} \frac{1}{T} \int_0^T x(t)y(t) dt = c$$

PROOF. By integrating the first equation of system (2) with from 0 to  $T$  we obtain

$$x(T) - x(0) = \int_0^T x(t) - x(t)y(t) dt.$$

Dividing by  $T$  and letting  $T \rightarrow \infty$  will force the left hand side to zero (since all trajectories are bounded) and we obtain:

$$\lim_{T \rightarrow \infty} \frac{1}{T} \int_0^T x(t)y(t) dt = \lim_{T \rightarrow \infty} \frac{1}{T} \int_0^T x(t) dt = c$$

This rather remarkable result implies that the time average of the product of species is equal to the product of the time averages. We will use this result in our analysis.

### 3 Scavenger Model on Classical Lotka-Volterra

We now introduce a scavenger species,  $z$ , into the two species predator prey system. We assume that the scavenger species,  $z$ , will die exponentially in the absence of any other species and will directly benefit in proportion to the number of deaths of  $x$  and  $y$  that occur naturally, as well as those caused by the predation of  $y$  on  $x$  (i.e. the kills). Our model is:

$$\begin{cases} \frac{dx}{dt} = x - xy, \\ \frac{dy}{dt} = -cy + xy, \\ \frac{dz}{dt} = -ez + fxyz + gxz + hyz - iz^2 \end{cases} \quad (3)$$

where,

- $e$  represents the natural death rate of the scavengers,
- $f$  represents the benefit to the scavenger by scavenging corpses of the prey killed by the predator,
- $g$  represents the benefit to the scavenger by scavenging corpses of the prey who die naturally,
- $h$  represents the benefit to the scavenger by scavenging corpses of the predator who die naturally,
- $i$  is associated with the carrying capacity of the scavenger.

Notice that the cubic interaction term makes this system a non-quadratic system (i.e., not a generalized Lotka-Volterra system). The quadratic term  $iz^2$  is necessary, otherwise the scavenger population can grow without bound. After a simple change of variables, system (3) can be transformed to a system of the form:

$$\begin{cases} \frac{dx}{dt} = x - xy, \\ \frac{dy}{dt} = -cy + xy, \\ \frac{dz}{dt} = -ez + fxyz + gxz + hyz - z^2 \end{cases} \quad (4)$$

(i.e., we can assume that  $i = 1$ ). The fact that the equations involving  $x$  and  $y$  are uncoupled to  $z$  imply that the trajectories of the system are trapped on the family of

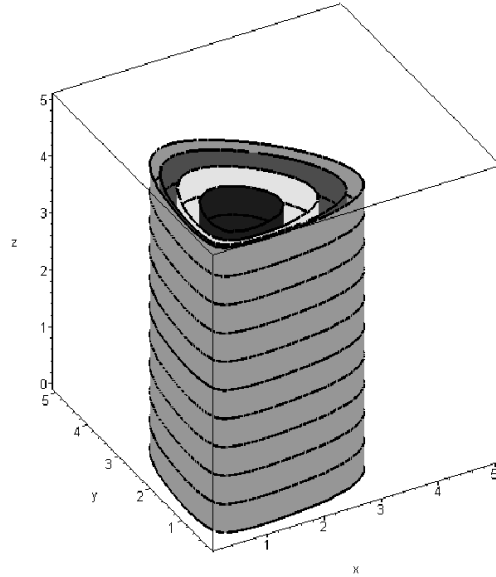


Figure 2: Various invariant cylinders of system (2).

cylinders given by  $\ln y - y + c \ln x - x = C$  (see Figure 2). These trajectories wind around the cylinders as the dynamics of  $(x(t), y(t))$  are governed by system (2).

For any positive initial condition,  $(x_0, y_0, z_0)$  with  $(x_0, y_0) \neq (c, 1)$ , the behavior of  $(x(t), y(t))$  is periodic with period  $T$  ( $T$  is a function of  $C$  above). Define  $z_k = z(kT)$ . From the Intermediate Value Theorem and the fact that trajectories of an autonomous system cannot cross, the sequence  $\{z_k\}$  is either increasing, decreasing or constant. Note that the system has a fixed point  $(c, 1, -e + fc + gc + h)$  which is in positive space when  $-e + fc + gc + h > 0$ .

The following theorem characterizes all trajectories in system (4) (and hence system (3)).

**THEOREM 3.1**

1. For  $-e + fc + gc + h \leq 0$ , all trajectories in positive space limit to a Lotka-Volterra solution in the  $z = 0$  plane, i.e. the scavenger goes extinct;
2. For  $-e + fc + gc + h > 0$ , on each invariant cylinder  $\ln y - y + c \ln x - x = C$ , there exists exactly one periodic trajectory in positive space to which all trajectories on that cylinder tend (See Figure 3).

**PROOF.** For any fixed positive  $(x_0, y_0) \neq (c, 1)$ , let  $T$  be the period of the corresponding periodic solution in the  $xy$ -plane. Integrating  $\frac{z'(t)}{Tz(t)}$  from 0 to  $T$  and using Lemma 2.1 and the averaging formulas that appear above it, we obtain

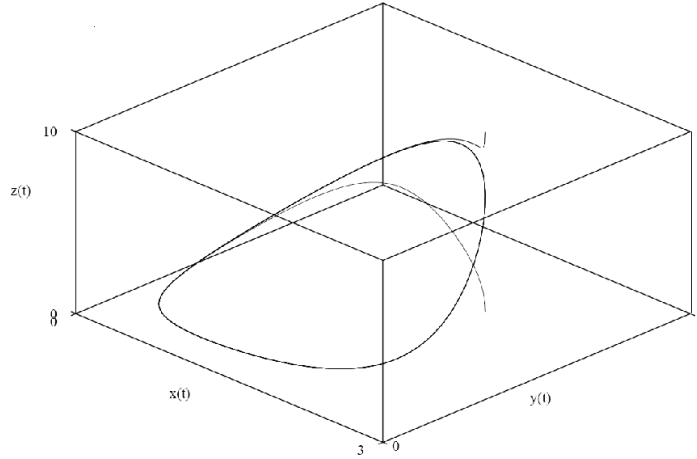


Figure 3: Two trajectories in 3-space of system (5) with initial conditions on the same cylinder.

$$\frac{1}{T} \ln\left(\frac{z(T)}{z_0}\right) = -e + fc + gc + h - \frac{1}{T} \int_0^T z(t) dt.$$

In particular, for  $-e + fc + gc + h \leq 0$  we have that  $z(T) < z_0$  which implies that  $\{z_k\} = \{z(kT)\}$  is decreasing. The sequence  $\{z_k\}$  cannot tend to a positive limit since the left hand side of the equation above could be made arbitrarily close to zero while the right hand side remains bounded away from zero, giving a contradiction.

For the case  $-e + fc + gc + h > 0$ , notice that for positive initial conditions  $(x_0, y_0, z_0)$  and  $(x_0, y_0, \tilde{z}_0)$  with  $\tilde{z}_0 > z_0$  we have  $\tilde{z}(t) > z(t)$  for all  $t$  so  $\int_0^T \tilde{z}(t) dt > \int_0^T z(t) dt$ . This implies that for fixed  $(x_0, y_0)$ , the map  $z_0 \rightarrow \int_0^T z(t) dt$  is monotone increasing, unbounded, and continuous in  $z_0$  and is equal to 0 for  $z_0 = 0$ . Hence, by the intermediate value theorem, there exists exactly one  $z_0^*$  so that  $\frac{1}{T} \int_0^T z(t) dt = -e + fc + gc + h$ . For the initial condition, we have

$$\frac{1}{T} \int_0^T \frac{z'(t)}{z(t)} dt = 0$$

which implies that  $z(T) = z(0)$ , giving a periodic orbit.

If  $z_0 < z_0^*$ , we have  $\frac{1}{T} \int_0^T z(t) dt < -e + fc + gc + h$  and for  $z_0 > z_0^*$  we have  $\frac{1}{T} \int_0^T z(t) dt > -e + fc + gc + h$ . Hence, for initial conditions  $(x_0, y_0, z_0)$  with  $z_0 < z_0^*$  we have

$$\frac{1}{T} \int_0^T \frac{z'(t)}{z(t)} dt > 0$$

which implies that  $z(T) > z_0$  and the reverse if  $z_0 > z_0^*$ .

Thus the trajectory starting at  $(x_0, y_0, z_0 < z_0^*)$  spirals up toward the periodic orbit. If  $z_0 > z_0^*$ , then the trajectory spirals down to the periodic. Since the point  $(x_0, y_0, z_0)$

was arbitrary, we see that all trajectories must tend to a periodic orbit except for starting points of the form  $(c, 1, z_0)$ , which tend to the equilibrium  $(c, 1, -e+fc+gc+h)$  along the equilibrium's one-dimensional stable manifold.

The above theorem completely characterizes all trajectories in positive space for any initial conditions. The scavenger persists if  $-e + fc + gc + h > 0$  and, in the long term, tends to oscillate periodically with the same period as the predator/prey and with a shift in phase (unless  $x$  and  $y$  begin at equilibrium). When  $-e + fc + gc + h \leq 0$ , the scavenger species cannot sustain itself on the carcasses of the predator and prey (see Figure 4).

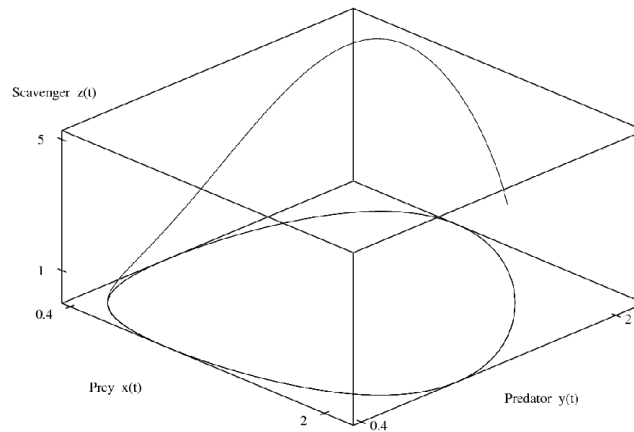


Figure 4: A trajectory where  $-e + fc + gc + h \leq 0$ , exhibiting extinction of  $z$ .

## 4 Conclusions and Further Work

In this paper, we have suggested a natural model that incorporates a scavenger species into a predator-prey scenario. The fact that the predator and prey are not affected by the scavenger allows the model to be completely characterized mathematically. This simplification may also be biologically relevant for some choices of species where the scavenger's presence would not affect either the predator or prey. This model demonstrates biologically acceptable results for a robust set of parameter values with a sustainable scavenger species when  $-e + fc + gc + h > 0$  and extinction otherwise. With this baseline model in hand, one can generalize this system in many ways. First, by analyzing the impact of a scavenger that in some way competes with the predator or prey for resources. Also, seasonal effects or alternative interaction terms could be introduced. We hope to investigate generalizations in future work.

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