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The Use of a Kernel Ecological System in a Multi Species Predator-Prey Model and Climate Change Impact on Biodiversity

ROBERTO N. PADUA
rnpadua@yahoo.com
Liceo de Cagayan University

DEXTER S. ONTOY
dexter_s_ontoy@yahoo.com
Cebu Normal University

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Abstract - The interaction of multiple species of animals in an ecological system is modeled by first reducing the ecological system to a kernel ecological system consisting of keystone species and top predators in the environment through Graph Theory. From the reduced kernel ecological system of keystone species, a system of Lotka-Volterra differential equations is used to describe the predator-prey relationships that exist. The equations for the number of organism per species were derived and additive environmental stochasticity or noise is added to each equation. The noise is assumed to come from an extreme value distribution or Gumbel distribution to reflect the impact of extreme weather conditions on the population dynamics of the entire ecological system. Results reveal a rich dynamical behavior for the system which otherwise would not have been revealed by straight application of deterministic predator-prey models.

Keywords - predator, prey, graph theory, Lotka-Volterra, multi-species model, stochastic model

INTRODUCTION

Predator-prey models are important tools used in describing the population dynamics of animal populations. The most commonly used model is the Lotka-Volterra system of differential equations (Rainville and Bedient 1987) for a two-animal system which could easily be extended to a multi-species model. The busts and booms of animal populations are, for a large part, accounted for by the natural processes of predation, death, birth, and density-dependence. The International Panel of Climate Change (IPCC) estimates that for every 1^{o} rise in global temperature, 3% of animal species become extinct (IPCC, 2010). The interaction of population-regulating parameters (i.e. birth, death, predation) had been studied in the past (Brauer & Castillo-Chavez 2000) but the interaction of these with climate change or environmental change has not been dealt with extensively in the literature.

We attempt to: a) generalize the classical Lotka-Volterra System of differential equations using directed graphs as basis for the formulation of the equations, b) input environmental stochasticity as an additive component in the solution vector in (a) using an extreme-value distribution, and c) analyze the interactions of population-regulating parameters and environmental changes via simulation and Monte Carlo methods. Almost all mathematical models involving the Lotka-Volterra system of differential equations deal exclusively with deterministic events when in reality, the complex interactions that occur in real-life can be best described in terms of a stochastic model. This is the strength of the present approach. Moreover, the large number of species involved in a food web makes modeling by differential equations untenable when individual species is considered. This study also makes further simplification of an ecological system by modeling only the behavior of "keystone" species and top predators which are

found by using methodologies from graph theory. For instance, an ecological system consisting of hundreds of species can be reduced to a kernel interaction model of may be 3 to 4 keystone species. Necessary and sufficient conditions for the long term survival of all of the species in the ecosystem are derived based on the behavior of the kernel ecological subsystem.

THE CLASSICAL TWO-SPECIES LOTKA-VOLTERRA MODEL

The Lotka–Volterra predator–prey model was developed by Alfred J. Lotkain the context of the theory of auto-catalytic chemical reactions" in 1910. In 1920, Lotka tried out the model to biological systems using a plant species and an herbivorous animal species as an example and in 1925 he utilized the equations to analyze predator-prey interactions in his book arriving at the equations discussed below. Vito Volterra, made a statistical analysis of fish catches in the Adriatic independently to verify the validity of the Lotka's model in 1926.

C.S. Holling further extended this model, in two papers in 1959, where he proposed the idea of a functional response. Both the Lotka-Volterra model and Holling's extensions have been used to model the moose and wolf populations in Isle Royale National Park. It is one of the best studied predator-prey relationships with over 50 published papers dealing with the two animal populations.

We re-state the classical Lotka-Volterra Model for a two-species system here for convenience. Let:

$X(t)$ = number of prey at time t;
$Y(t)$ = number of predators at time t;
β_i = birth rate of the i^{th} species i=1,2
δ_i = death rate of the i^{th} species i=1,2
η = interaction rate between $X(t)$ and $Y(t)$ leading to the predation of $\eta X(t)$ preys
$N(t) = X(t) + Y(t)$ for $t \in T$, a time index.

The rate at which the population of preys changes is given by:

$$\frac{dX}{dt} = \beta_1 X(t) - \delta_1 X(t) - \eta X(t) Y(t) \qquad [1]$$

i.e. the population of preys changes due to birth, death and predation.

The rate at which the population of predators changes is:

$$\frac{dY}{dt} = \beta_2 Y(t) - \delta_2 Y(t) = (\beta_2 - \delta_2) Y(t) \qquad [2]$$

i.e. the population of predators changes due to birth, natural death only, assuming that the predators are not preyed upon by other species. This is a simplified Lotka-Volterra Model which, from [2], yields the solution:

$$Y(t) = C\exp(\beta_2 - \delta_2)t \qquad [3]$$

and assuming that Y(0) is the predator population at time t =0, we have:

$$Y(t) = Y(0)\exp(\beta_2 - \delta_2)t \qquad [4]$$

We can now plug in Equation [4] to [2] to obtain:

$$\frac{dY}{dt} = \beta_1 - \delta_1 \eta Y(0)\exp(\beta_2 - \delta_2)t)X(t) \qquad [5]$$

Equation [5], of course, is variable separable:

$$\frac{dX}{Xt} = [\beta_1 - \delta_1 \eta Y(0)\exp(\beta_2 - \delta_2)t]dt \qquad [6]$$

In the succeeding discussion, we let K = ηY(0). Thus:

$$\ln X(t) = (\beta_1 - \delta_1)t - K\int \exp(\beta_2 - \delta_2)t dt + C_1 \qquad [7a]$$

$$= (\beta_1-\delta_1)t\text{-}k.\ \frac{\exp(\beta_2-\delta_2)t}{(\beta_2-\delta_2)} + C_1 \qquad [7b]$$

Hence:

$$X(t) = C_1 e^{(\beta_1-\delta_1)t - K.\frac{\exp(\beta_2-\delta_2)t}{(\beta_2-\delta_2)}} \qquad [8]$$

In normal situations, $\beta_{i>}\ \delta_i$ for all i, that is, there will be more "births" than "deaths" ensuring the continuity of species. The decline in the population of preys can then be attributed to the intensity of predation K. The number of preys will continue to grow provided:

$$K \leq (\beta 1 - \delta 1)(\beta 2 - \delta 2)\exp\left(-(\beta 2 - \delta 2)\right) \quad [9]$$

Otherwise, the preys will become extinct. Notice that the rate of interaction K is highly affected by population densities, i.e., the probability that a prey encounters a predator is higher for denser populations.

Assumptions of the Lotka-Volterra Model

The Lotka-Volterra model has a number of assumptions about the environment and dynamic behavior of the predator and prey populations:

1. The prey population finds sufficient food at all times.
2. The food supply of the predator population is entirely dependent on the prey populations.
3. The rate of change of population is proportional to its size.
4. During the process, the environment does not change in favors of one species and the genetic adaptation is sufficiently slow.

Since differential equations are used, the solution will be purely deterministic and continuous. This, in turn, implies that the generations of both the predator and prey are continually overlapping.

Addition of Environmental Stochasticity

The solutions (4) and (8) can now be modified to account for environmental stochasticity:

$$X^*(T) = X(t) + \epsilon(t) \qquad [9a]$$
$$Y^*(t) = Y(t) + \epsilon(t)$$

where $\epsilon(t)$ are independent and identically distributed random environmental noise assumed to come from the Gumbel or extreme value distribution G(.). The choice of the Gumbel distribution is consistent with the intent of examining the population dynamics during climate change or extreme weather disturbances.

MULTI-SPECIES INTERACTION MODEL

We depict a food web by means of *nodes* and *edges* representing *species* and *interaction*, respectively. In the language of Graph Theory, we have a graph consisting of vertices V and edges E, denoted by G(E,V). The vertices and the edges have some form incidence relation. The graph representing the food web in this study belongs to the category of directed graphs. Arrows going into the node represents number of species predating that organism, while arrows going out represent species being preyed upon by the other species. The difference in the number of arrows going in and going out of a node is called the *valence* of the node.

Fig. 1 shows a 7-species interaction in an ecological system (food web):

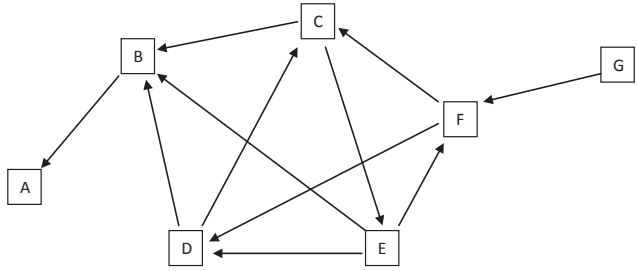

Fig. 1. Species Interaction in a System (Food Web)

Based on the species interaction shown in Fig. 1, different consequences will be observed when a species is removed from the system. If C is removed, B will have a positive valence because one predator is removed effectively increasing the size of B, D will have a negative valence because D loses a food source, E will have a positive valence, F will have a negative valence.

Hence:

Valence of C = +B –D +E –F = 0.
Computations for the rest are similarly done.
We can simplify the analysis by letting:
$V_i = I_i - O_i$;

where:

V_i = valence of the i^{th} organism
I_i = the number of arrows going into the node (number of species eating the i^{th} species)

O_i = the number of arrows going out of the node (number of species being eaten by the i^{th} species)

Thus:

V_i = positive when $I_i > O_i$;
= zero when $I_i = O_i$; and
= negative when $I_i < O_i$.

In terms of this formulation, we can analyze the effects of removing a species from the food web as we have earlier done but now formulated in terms of valences. For instance, the valence of C is zero because there are equal number of arrows going in and out of the node C. What this means in reality is that the removal of species C from the system does not have any effect on the species sizes of the other organisms. On the other hand, the valence of node B is two (2) because there are three arrows going into B but only one arrow going out of

it. This means that if we remove B, then the sizes of the other species will be drastically affected because B is the food of three species in the system. Therefore, the following can be concluded:

1) species with positive valence will induce a change in the system, either on the existence of the i^{th} species or the population of the i^{th} species;

2) species with zero valence has no effect on the system; and

3) species with negative valence are the **top predators** in the system.

Species belonging to category (1) will be called **keystone species** because of their impact on the sizes of the other species in the system. We will not be so much concerned with species belonging to category (2) because they have no discernible effect on the other species. We define the kernel of an ecological system as the set:

Ker(E) = { keystone species, top predators}.

The kernel of an ecological system, ker(E), provides all the information needed to analyze the long term performance of all the other species in the ecological system itself. Thus, ker(E) provides a convenient summary of the multi-species interactions that occur in the whole ecosystem.

MULTI-SPECIES INTERACTION MODEL FOR Ker(E)

Consider next the interaction of the species in kernel of the ecological system. For convenience, we use the same illustration as Fig. 1. The kernel of this ecological system is: ker (E) = {B,E,G}:

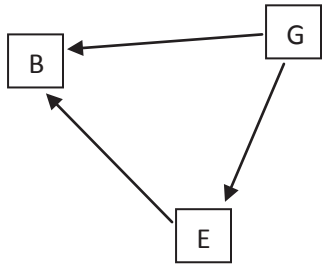

Fig. 2. Kernel of the 7-Species Ecological System.

If we remove species G from the system, this will result into positive valences for both species B and E because the removal of a predator will consequently increase both their populations. On the other hand, if we remove species E, species G will have a negative valence due to the removal of its prey. The removal of the same species E, however, will result into positive valence for species B because this removes one of its predators. However, if we remove species B, it will cause negative valences for both species E and G because species B is their common food. If this happens, the entire system will ultimately collapse.

The Lotka-Volterra differential equations describing this system are:

$$dB/dt = \beta_1 B(t) - \delta_1 B(t)E(t) - \delta_2 B(t)G(t) - \delta_3 B(t) \quad [11]$$
$$dE/dt = \beta_2 E(t) - \delta_4 G(t)E(t) - \delta_5 E(t)$$
$$dG/dt = \beta_3 G(t) - - \delta_6 G(t)$$

The rate at which E(t) changes with respect to G(t) is obtained from:

$$dE/dG = dE/dt/dG/dt = \frac{[(\beta_2 - \delta_5) - \delta_4 G]\ E}{(\beta_3 - \delta_6)G}$$

from which we derive:

$$E(t) = [G^{\theta}](\exp(-\delta_4 G(t)] \text{ where } \theta = \frac{[(\beta_2 - \delta_5)}{(\beta_3 - \delta_6)} \quad [12]$$

As the number of top predators G(t) increase without bound ($G(t)\to\infty$), we note that the number of species E tends to zero ($E(t)\to 0$) because the rate of predation δ_4 remains constant and positive. This is exactly what will happen if the birth rate of the top predators G(t) exceeds the death rate and predation rate is constant. Similarly, once the alternative food of G(t) (namely, E(t)) is exhausted, the predator G(t) turns to B(t) and the relationship (12) holds for B(t) and G(t) also. Thus, B(t) will also be exhausted. This leaves only the top predator in the system. Since both E(t) and B(t) are zero, the population G(t) will soon be wiped out due to starvation (resource limitation).

Suppose that a conservation measure is adopted to ensure the survival of the species in the system. Such a conservation effort must focus on the keystone species B as we now demonstrate. The following conditions are *necessary* to ensure the survival of the species in the system:

1. The quantity $a = \beta_1 - \delta_3$ which is the difference between the birth rate and the natural death rate of species B must exceed $b = \beta_2 - \delta_5$ (the difference in the birth rate and natural death rate of species E) and $c = \beta_3 - \delta_6$ (the difference in the birth rate and natural death rate of species G);
2. The rate of interaction or predation of G on E must be less than b. Equivalently, condition [9] must hold.

If in addition to these necessary conditions, we also impose a sufficiency condition, namely, that the quantity a is related to b and c as follows: $a > b + c$, then all the species in the system will survive indefinitely.

The first necessary condition ensures that there will always be enough number of species B which will serve as food (prey) of the other species in the kernel. The second necessary condition ensures that E will survive. The sufficient condition which says that the number of species B is greater than the number of species E plus the number of species G ensures that the species survive in perpetuity. Survival of all the species in the kernel of the ecosystem ensures survival of all the other species outside of the kernel.

The obvious next question is to identify conservation measures that satisfy both the necessary and sufficient conditions for species

survival. We can provide general features of "optimal" conservation measures that satisfy the criteria above:

1. Conservation measures must target keystone species in an ecosystem. Conservation efforts that attempt to conserve multiple species, even those whose valence is zero, are far more difficult to implement in practice without resistance from stakeholders. This means that national government policy-makers need to consult expert biologists whenever such an effort is to be launched.
2. Conservation measures need to ensure survival of the kernel species in the ecosystem. Conservation efforts, such as declaring a large area as a protected or reserved area, must make sure that the kernel species in the ecosystem are indeed going to survive. In other words, even if we undertake a shot-gun approach of protecting all species (including those not found in the kernel of the ecosystem) there is no assurance that the species will survive in the long run if the control parameters for the kernel species are not observed. This is scientifically proven by the systems of differential equations derived.
3. Finally, all conservation efforts must be rooted in science. Otherwise, such efforts will only result in needless conflicts without achieving their desired goals.

SIMULATION SET-UP AND RESULTS

The purpose of this section is to provide some numerical calculations to illustrate the impact of climate change on the dynamics of the predator-prey relationships that occur in a multi-species ecosystem. The 7-species "small world" ecosystem used to derive the various differential equations and valences served as the basis for the simulation experiments. Two (2) simulation set-ups are established, the deterministic set up and the stochastic set up.

Deterministic Set-Up

The regulating parameters for the population dynamics of the

species found in the kernel ecological subsystem are fixed such that no abrupt or catastrophic events are expected. For this experiment, we set:

$a = \beta_1 - \delta_3 = 0.8$ which is the difference between the birth rate and the natural death rate of the keystone species B

$b = \beta_2 - \delta_5 = 0.4$ (the difference in the birth rate and natural death rate of species E) and

$c = \beta_3 - \delta_6 = 0.2$ (the difference in the birth rate and natural death rate of the top predator G)

$\delta_1 = 0.5$, $\delta_2 = \delta_4 = 0.2$ (the predation rates)

We simulated the population growth/changes over t = 100 generations. At time t= 0, we assumed that there are equal number of individuals (n = 10) for species B,E and G. We solved the system of differential equations earlier presented and put the result in a logistic sigmoidal form:

$G(t) = G(0) \exp(ct)$
$E(t) = E(0) \exp[bt - \theta\exp(ct)]$ where $\theta = \delta_4/c\, G(0)$
$B(t) = B(0) \exp[at - \delta_2/cG(0) \exp(ct) - \delta_1 E(0) \int \exp(bt - \theta\exp(ct))\, dt]$

The integral expression for the function B(t) was approximated by a fourth-order Maclaurin's polynomial.

Stochastic (Monte Carlo) Set Up

The stochastic model for the Lotka-Volterra predator-prey equations is obtained by simply adding a random noise to the equation for the keystone species B while the population growths of the top predator G and secondary predator E follow a time-delay feedback system. This means that species E follow the growth curve of its prey , species B, but with a time delay Δt, that is, it takes Δt time before the population of predators feels the loss of its prey. The noise or error

terms are obtained from the smallest extreme value distribution or the Gumbel distribution with location parameter 0 and scale parameter 2.

Results:

As shown in Fig. 3, the population size of species B is smaller than that of species G at t=1. However, there is a reversal between t=5 and t=6 wherein the population size of species B becomes larger than that of species G (the intersection implies that the population size of both species are equal) due to faster growth rate of species B than that of species G. Species B reaches maximum (N=10) at t=12, while species G reaches its maximum t=50. On the other hand, species E has the smallest population at t=1, capping at t=62.

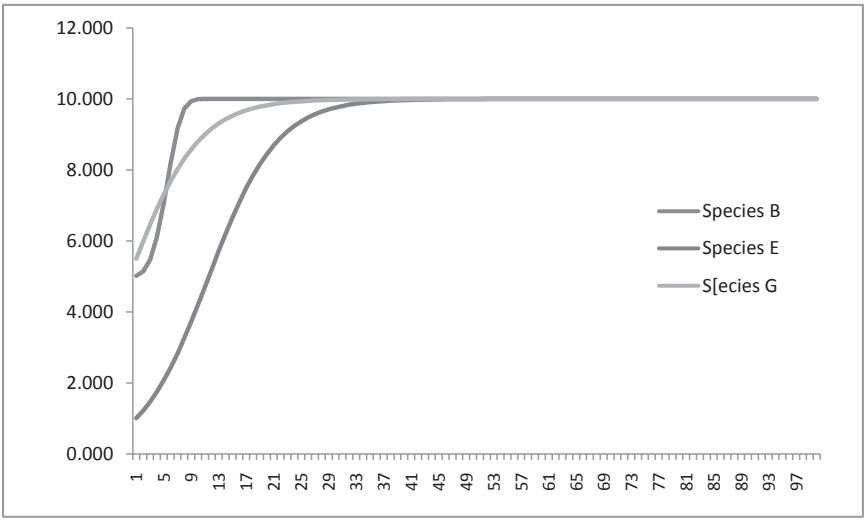

Fig. 3. Population of species B, E and G at time t.

This pattern has implications on biodiversity conservation:

1) Slower growth rate for both species E and G would ensure the existence of species B;
2) Given the faster growth rate of species B (than both species E and G), the ecosystem would be dominated by them thus

minimizing the interaction between E and G. This would then reduce the possibility of species E being wiped out due to its predation by G. In the absence of species B, however, slower growth rate of species E than species G would ultimately result in the annihilation of the former (species E will become extinct due to predation).

3) This pattern further validates the importance of focusing conservation efforts to keystone species (as represented by species B) if we want to maintain higher biodiversity.

Stochastic (Monte Carlo) Results

Let us now consider environmental nuisance (i.e. environmental factors such as temperature changes brought about by climate change) which affect the population size of species B and E in the natural systems. In the simulation, we included a time lag of $\Delta t=2$ for the predator's population changes. As shown in Fig. 4, environmental nuisance led to the stochasticity of the population size of both species.

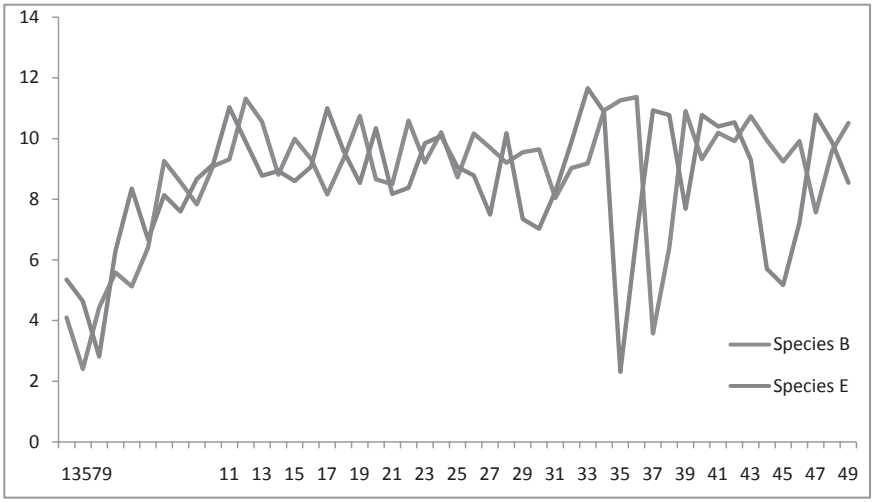

Fig. 4. Stochastic Population Sizes of Predator (E) and Prey (B).

When the population of predators (E) is high, the population of the preys (B) is low since many of the preys are consumed by the predators. It is, however, unclear which one drives the population size of the other. Perhaps, a mutual feedback mechanism may effectively explain the outcomes of the experiment. Drops in the population levels of species E are followed by drops in the population of species B after the specified time lag, that is, when the predator population dips, they begin to compensate by consuming more of the prey so that after the specified time lag, the prey population also dips low. Shortages in food supply (species B) takes about two time lags before being felt by the consumers (predator E). The environmental factor (climate change) drives the population levels of the prey population B in a rather erratic and irregular trajectory over time. The environmental nuisance factor, in fact, had caused a collapse in the predator population at t=35 followed by a collapse in the prey population at t=37. Note that this phenomenon is not expected in the ideal world of pure predator-prey interaction or the deterministic model. Note, likewise, that at the lowest point in the predator population (species E at t=35), the number of preys is highest which inevitably signals that the population of preys would be decimated by over-predation after two time lags. The strong interaction of environmental noise and predation caused the collapse of the prey population.

Next, we consider impact of environmental factors on species B and E in the natural system, this time with the top predator (species G). The population also follows erratic and irregular trajectory.

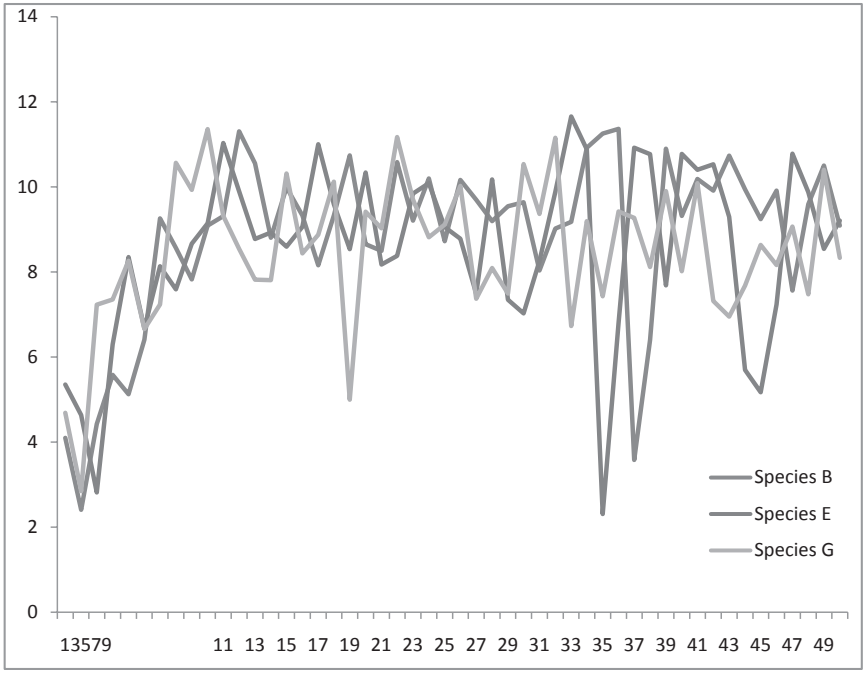

Fig. 4. Stochastic Population Sizes of Predators (E and G) and Prey (B).

When the population of species B dropped at t=5, there was a corresponding drop in the population of both species E and G at t=7 (time lag of $\Delta t=2$). The drop in the population of the prey resulted in the drop of the population of both E and G. Interestingly, the effect of climate change is significant on species G compounded with the drop in the population of the prey species (t=18). The top predator G is the last species to feel the adverse impact of climate change as the graph clearly demonstrates. The analogy to the human species is almost trite viz. human beings will feel the effects of climate change last, perhaps, at a time when it is too late to respond appropriately.

CONCLUSIONS

The classical deterministic predator-prey interaction model of Lotka-Volterra, even when extended to a multi-species model, is insufficient to explain the population dynamics of species in an ecosystem. A stochastic component, to incorporate the impact of climate change, has to be considered. The study has demonstrated that a stochastic kernel sub-ecosystem can realistically model the population dynamics of animal species in an ecological system through the use of graph theory, differential equations and statistical modeling. When applied in a "small-world" ecosystem results have shown that climate change can have catastrophic effects on keystone species and subsequently, on the predators of the ecosystem. Effects on individual species, however, are difficult to predict i.e. some species actually increase in size with climate change, thus, disrupting the normal flow in a food web.

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