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Sensitivity Analysis of Parameters in a Competition Model

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Abstract: Competition models may be used by ecologists as basic guidelines in analyzing issues that contribute to the decline of species population. To be used for that purpose, a mathematical model must be prudently parameterized. Therefore, this paper examines the effects of interference competition by lions with human–related mortality to the population dynamics of African wild dogs. The model was carefully parameterized and validated with estimated data by employing the theory of basic reproduction number and by running the sensitivity analysis. Numerical simulation of the model was executed by using MATLAB to explore the outcome of certain key parameters when changes are applied on them.

Keywords: Interference Competition, African Wild Dog, Lion, Basic Reproduction Number, Sensitivity Analysis

1. Introduction

The African wild dog was formerly present throughout sub-Saharan Africa, although it was never locally abundant. This species is today restricted to fragment population mainly in southern and eastern Africa (Woodroffe et al., 1997). Potentially viable populations currently exist in Botswana, Kenya, Mozambique, South Africa, Tanzania, Zambia and Zimbabwe (Sillero-Zubiri et al., 2004).

The status of the African wild dog is classified as endangered (EN) (IUCN Red List, 2008). Wild dogs have declined across their range; they are now extinct in 25 of the 39 countries in which they were formerly recorded, with the total population estimated to be 5,750 individuals in not more than 1,000 packs (Woodroffe et al., 2004) cited by (Dutson and Sillero-Zubiri, 2005).

Competition is defined as a negative interaction that occurs among organisms whenever two or more organisms require the same limited resource (Cronin and Carson, 2015). While, Interference competition is defined as direct interactions between organisms that decrease use of the common resources (Park, 1954) cited by (Nakayama and Fuiman, 2010).

A study in Australia conducted by (Caut et al., 2007) on rats and mice they employed a classical Lotka – Volterra two species competition model and they named the model as the Competitor Release Effect. They assumed that a rat is globally a better competitor over the mouse either by better exploiting resources or by generally winning interference interactions. They called rat species the superior competitor and the mouse species the inferior competitor. According to Caut et al. (2007), an inferior competitor can increase in numbers if the superior is controlled, due to the competitive interactions between them.

On the other hand, Blanco et al. (2014) studied population dynamics of wolves and coyotes at Yellowstone National Park, and the study was titled as modeling interference competition with an infectious disease. The goal of the study was to understand how different factors may affect the decline in population size of a dominant predator, the wolf and a subordinate predator, the coyote in relation to human-related mortality, disease and other factors.

Caut et al. (2007) studied a two species competition model which have twelve parameters but authors do not explain how they came up with most influence parameters in their model. Moreover, Blanco et al. (2014) studied an interference competition with an infectious disease, whereby this disease component was a reason of employing basic reproduction number for their model's sensitivity analysis.

Therefore, having noted that, and with exception that our competition model does not have disease component, we studied a competition model by evaluating and analyzing the sensitivity indices of the basic reproduction number (R_0) in order to determine the importance of each parameter in the competition model. However, the intention is to simplify the work of numerical analysis by considering parameters that bring much effect in the model.

2. Model Formulation

The mathematical model for two competing species with human-related mortality to the species is formulated in this section.

2.1. Assumptions

In order to formulate the models, the following assumptions were made:

- The lions and African wild dogs species live in an ecosystem where external factors such as droughts, epidemics are stable or have similar effect on the competing species;
- There is no African wild dog related mortality to lions;
- Lions kill African wild dogs to eliminate number of threats and competition;
- African wild dogs and lions are both victims to humans.

2.2. Mathematical Model

A nonlinear mathematical model is formulated and analyzed.

$$\frac{dN_1}{dt} = r_1 N_1\left(1 - \frac{N_1}{K_1} - \alpha_{12}\frac{N_2}{K_1}\right) - \eta_1 N_1 - \delta N_1 N_2 \qquad (1)$$

$$\frac{dN_2}{dt} = r_2 N_2\left(1 - \frac{N_2}{K_2} - \alpha_{21}\frac{N_1}{K_2}\right) - \eta_2 N_2 \qquad (2)$$

where $r_1, r_2, K_1, K_2, \alpha_{12}$, and α_{21} are all positive constants and α_{12} and α_{21} measure the competitive effect of N_2 on N_1 and N_1 and N_2 respectively and that $\alpha_{12} > \alpha_{21}$.

This model is modified from the classical Lotka-Volterra competition model as provided by (Baigent, 2010) in his lecture notes on Introduction to Lotka-Volterra Dynamics.

Table 1. *Parameters used in the Competition model (1) – (2).*

Parameter	Description	Value
η_1	rate of mortality caused by human beings to African wild dogs	0.0005
η_2	rate of mortality caused by human beings to lions	0.0001
δ	rate of mortality caused by lions to African wild dogs	0.00076
α_{12}	competition coefficient of lion species on wild dog species	1.00014
α_{21}	competition coefficient of wild dog species on lion species	0.039
K1	carrying capacity for African wild dogs	5800
K2	carrying capacity for lions	1020
r_1	population growth rate of African wild dogs	0.05
r_2	Population growth rate of lions	0.025

Table 2. *Variables used in the Competition model and their initial values.*

Variables	Description	Initial Value
N_1	Population of African wild dogs	580
N_2	Population of lions	48

On the other hand, we have chosen classical Lotka-Volterra competition model for the reason that, it is a standard model for interference and exploitative categories of competition phenomenon. Besides, to the best knowledge of the authors, the Lotka-Volterra competition model has not yet been employed to study competition between African wild dog and lion species. Therefore, we have used that opportunity to use the model for these two competing species.

However, we have modified the classical Lotka-Volterra competition model by adding the following components: the rate of mortality caused by human to the competing species (η_1 and η_2) and the rate of mortality caused by lions to African wild dogs (δ). We have modified the model in this way for the reasons that, the wild dog species are endangered (IUCN Red List, 2008) and major threats to their existence are human and lion species (WWF, 2014; Perry, 2014).

3. Sensitivity Analysis

3.1. The Basic Reproduction Number, R_0

For the sake of conducting sensitivity analysis we have borrowed the concept of basic reproduction number, denoted by R_0 from epidemiological modeling but with the same concept that, R_0 should be less than unity so that the population under consideration can withstand.

The basic reproduction number R_0 of the model (1) and (2) is calculated by using the next generation matrix of an ODE (van den Driessche and Watmough, 2002). The R_0 is obtained by taking the dominant eigenvalue of FV^{-1}, whereby;

$F = \frac{\partial fi}{\partial N_1}$ and $V = \frac{\partial v_i}{\partial N_2}$ for $i = 1, 2$

Then from model (1) and (2) when $\frac{dN_1}{dt} = \frac{dN_2}{dt} = 0$ we obtain:

$$r_1 N_1 - \frac{r_1 N_1^2}{K_1} - \frac{r_1 \alpha_{12} N_1 N_2}{K_1} - \eta_1 N_1 - \delta N_1 N_2 = 0$$

$$r_2 N_2 - \frac{r_2 N_2^2}{K_2} - \frac{r_2 \alpha_{21} N_1 N_2}{K_2} - \eta_2 N_2 = 0$$

Therefore if we let $f =$ wild dogs' killings and competition from lion species and $v =$ the rest of the components in the model (1) and (2).

Then, it implies that:

$$f = \begin{pmatrix} \frac{-r_1 \alpha_{12} N_1 N_2}{K_1} - \delta N_1 N_2 \\ 0 \end{pmatrix} = \begin{pmatrix} f_1 \\ f_2 \end{pmatrix} \text{ and}$$

$$v = \begin{pmatrix} -r_1 N_1 + \frac{r_1 N_1^2}{K_1} + \eta_1 N_1 \\ -r_2 N_2 + \frac{r_2 N_2^2}{K_2} + \frac{r_2 \alpha_{21} N_1 N_2}{K_2} + \eta_2 N_2 \end{pmatrix} = \begin{pmatrix} v_1 \\ v_2 \end{pmatrix}$$

Hence by using linearization method, the associated matrices are given by

$$F = \begin{bmatrix} \frac{\partial f_1}{\partial N_1} & \frac{\partial f_1}{\partial N_2} \\ \frac{\partial f_2}{\partial N_1} & \frac{\partial f_2}{\partial N_2} \end{bmatrix}$$

$$V = \begin{bmatrix} \frac{\partial v_1}{\partial N_1} & \frac{\partial v_1}{\partial N_2} \\ \frac{\partial v_2}{\partial N_1} & \frac{\partial v_2}{\partial N_2} \end{bmatrix}$$

We get

$$F = \begin{bmatrix} \frac{-r_1\alpha_{12}N_2}{K_1} - \delta N_2 & \frac{-r_1\alpha_{12}N_1}{K_1} - \delta N_1 \\ 0 & 0 \end{bmatrix}$$ and

$$V = \begin{bmatrix} -r_1 + \frac{2r_1N_1}{K_1} + \eta_1 & 0 \\ \frac{r_2\alpha_{21}N_2}{K_2} & -r_2 + \frac{2r_2N_2}{K_2} + \frac{r_2\alpha_{21}N_1}{K_2} + \eta_2 \end{bmatrix}$$

with

$$V^{-1} = \begin{bmatrix} \frac{-1}{r_1 - \frac{2r_1N_1}{K_1} - \eta_1} & 0 \\ -\frac{\frac{r_2\alpha_{21}N_2}{K_2}}{\left(r_1 - \frac{2r_1N_1}{K_1} - \eta_1\right)\left(r_2 - \frac{2r_2N_2}{K_2} - \frac{r_2\alpha_{21}N_1}{K_2} - \eta_2\right)} & \frac{-1}{-r_2 + \frac{2r_2N_2}{K_2} + \frac{r_2\alpha_{21}N_1}{K_2} + \eta_2} \end{bmatrix}$$

Therefore:

$$FV^{-1} = \begin{bmatrix} -\frac{-r_1\alpha_{12}N_2 - \delta N_2}{r_1 - \frac{2r_1N_1}{K_1} - \eta_1} - \frac{\left(\frac{-r_1\alpha_{12}N_1}{K_1} - \delta N_1\right)\left(\frac{r_2\alpha_{21}N_2}{K_2}\right)}{\left(r_1 - \frac{2r_1N_1}{K_1} - \eta_1\right)\left(r_2 - \frac{2r_2N_2}{K_2} - \frac{r_2\alpha_{21}N_1}{K_2} - \eta_2\right)} & -\frac{\frac{-r_1\alpha_{12}N_1}{K_1} - \delta N_1}{r_2 - \frac{2r_2N_2}{K_2} - \frac{r_2\alpha_{21}N_1}{K_2} - \eta_2} \\ 0 & 0 \end{bmatrix}$$

The eigenvalues of the product of FV^{-1} are:

$$\lambda_1 = \frac{\left(\frac{r_1\alpha_{12}N_2}{K_1} + \delta N_2\right)\left(r_2 - \frac{2r_2N_2}{K_2} - \frac{r_2\alpha_{21}N_1}{K_2} - \eta_2\right) + \left(\frac{r_2\alpha_{21}N_2}{K_2}\right)\left(\frac{r_1\alpha_{12}N_1}{K_1} + \delta N_1\right)}{\left(r_1 - \frac{2r_1N_1}{K_1} - \eta_1\right)\left(r_2 - \frac{2r_2N_2}{K_2} - \frac{r_2\alpha_{21}N_1}{K_2} - \eta_2\right)}$$

and $\lambda_2 = 0$

It follows that the reproductive number which is given by the dominant eigenvalue for model system (1) and (2) is:

$$R_0 = \frac{\left(\frac{r_1\alpha_{12}N_2}{K_1} + \delta N_2\right)\left(r_2 - \frac{2r_2N_2}{K_2} - \frac{r_2\alpha_{21}N_1}{K_2} - \eta_2\right) + \left(\frac{r_2\alpha_{21}N_2}{K_2}\right)\left(\frac{r_1\alpha_{12}N_1}{K_1} + \delta N_1\right)}{\left(r_1 - \frac{2r_1N_1}{K_1} - \eta_1\right)\left(r_2 - \frac{2r_2N_2}{K_2} - \frac{r_2\alpha_{21}N_1}{K_2} - \eta_2\right)}$$

If $R_0 < 1$, it means interaction between wild dogs and lions is minimal, hence, the rate of competition is very small and lion–related mortality to wild dogs is less or there is no such an incident and the rate of human–related mortality to the competing species is very small. Therefore, under these circumstances, the wild dog population will prevail from being endangered and start to increase in number. Whereas, if $R_0 > 1$, then, the status of wild dog species will change to being extinct.

3.2. Sensitivity Analysis of Model Parameters

Sensitivity analysis state how important each parameter is to the competition model. Besides, sensitivity analysis is normally used to determine the strength of model predictions to parameter values, since there can be errors in data collection and postulated parameter values. Moreover, it is used to determine parameters that have greater influence on R0 and the one that has less influence. Therefore, we need to calculate the sensitivity indices of the reproduction number R0 to each parameter in the model. The parameters and their respective indices are ordered from most sensitive to the least.

Besides, a highly sensitive parameter should be carefully estimated, because a small variation in that parameter will lead to large quantitative changes. An insensitive parameter, on the other hand, does not require as much effort to estimate, since a small variation in that parameter will not produce large changes to the quantity of interest (Mikucki, 2012).

Table 3. *Sensitivity indices of R_0 calculated at the baseline parameter values given in Table 1.*

S/N	Parameter	Sensitivity index
1	δ	$+0.9887826560$
2	α_{21}	$+0.02520896021$
3	η_1	$+0.01265822785$
4	α_{12}	$+0.01121734444$
5	η_2	$+0.0001118059794$
6	r_2	-0.0001118059846
7	K_2	-0.02783968922
8	K_1	-0.2643819014
9	r_1	-1.001440884

3.3. Definition

The normalized forward sensitivity index of R_0 that depends differentially on a parameter p is defined as (Chitnis *et al.*, 2008:

$$X_p^{R_0} = \frac{\partial R_0}{\partial p} \times \frac{p}{R_0}$$

By using the explicit formula for R_0, one can easily derive an analytical expression for the sensitivity of R_0 with respect to each parameter that comprise it. The obtained values are described in Table 3, which presents the sensitivity indices for the baseline parameter values in Table 1.

3.4. Interpretation of Sensitivity Indices

Commencing on Table 3, while being arranged in an order of most to least sensitive parameters, it shows that, if there is an individual increase amongst the parameters $\delta, \eta_1, \alpha_{12}, \alpha_{21}$ and η_2, while keeping other parameters constant, they tend to increase the value of $\mathcal{R}_0$, indicating that they increase pressure on already declined wild dogs' population as they have positive indices. However, for the parameters r_2, K_2, K_1 and r_1 when each increases while keeping other parameters constant, they decrease the value of $\mathcal{R}_0$, suggesting that they decrease pressure on the decline of wild dog population as they have negative indices.

3.5. Numerical Simulation Analysis

Here, we illustrate the analytical results of the study by carrying out numerical simulations of the model system (1) and (2) using the set of estimated parameter values given as shown below.

δ=0.00076, α_{21}=0.039, η_1=0.0005, α_{12}=1.00014, η_2=0.0001

r_2=0.025, K_2=1020, K_1=5800, r_1=0.05

The final time was $t_f = 100$ years, and computations were run in Matlab with the $ode45$ routine. This function implements a Runge–Kutta method with a variable time step for efficient computation. Figure 1 shows the solution to the system (1) and (2) with the baseline parameter values given in Table 1 for wild dogs and lions respectively.

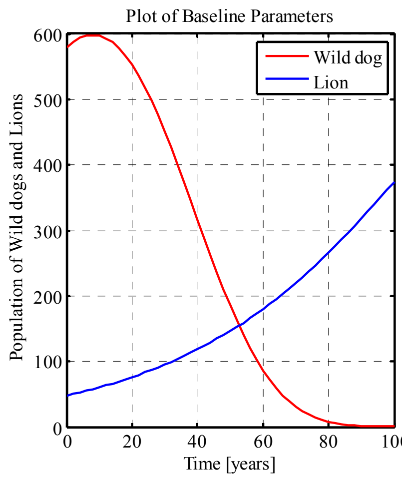

Figure 1. *Show variables of the ODE system (1) – (2) with baseline parameter values and initial variable values as in Table 1 and Table 2.*

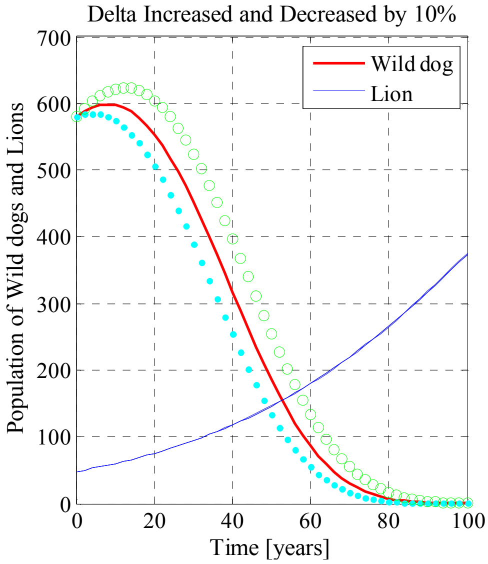

Figure 2. *Changes in the solution of the system (1) and (2) on increasing and decreasing the parameter value by 10 percent.*

Figure 2 shows a graph that reflects the effects on the population of wild dogs when delta, δ, was increased and decreased by 10 percent. The effect of increase in delta, δ, is shown by cyan dotted line which indicates that wild dog population will go to extinct in less than 80 years. Whereas, the effect of decrease in delta is shown by green dotted line, implying that wild dog population will die out in more than 80 years but less than 100 years. On contrary, when the parameter delta, δ, is decreased by 95 percent, wild dog population will grow and it will take more than 100 years to reach its carrying capacity, K_1, this is indicated by Figure 3. The obtained graphics support the sensitivity analysis prepared in section 3.2. The most positive sensitive parameter is the rate of wild dogs' mortality caused by lions, δ, where $X_\delta^{R_0} = +0 \cdot 9887826560$.

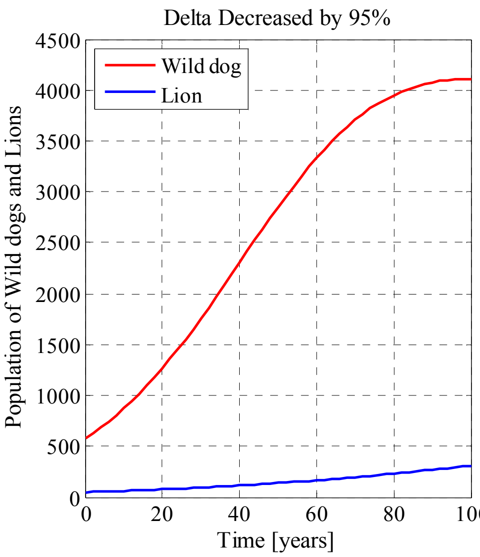

Figure 3. *Changes in the solution of the system (1) – (2) on decreasing the parameter value by 95 percent.*

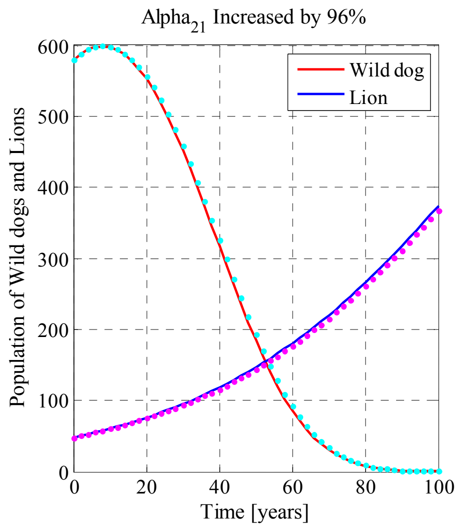

Figure 4. *Changes in the solution of the system (1) – (2) on increasing the parameter value by 96 percent.*

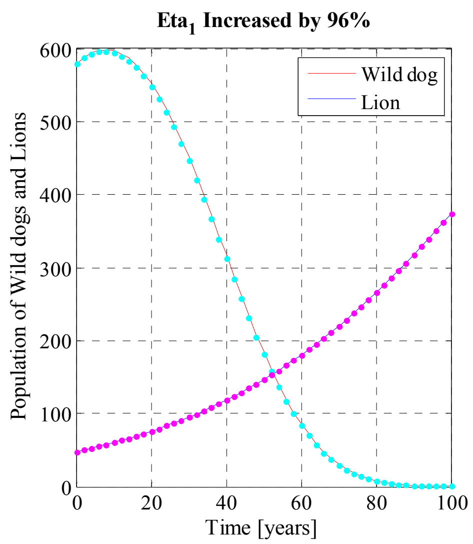

Figure 5. *Changes in the solution of the system (1) – (2) on increasing the parameter value by 96 percent.*

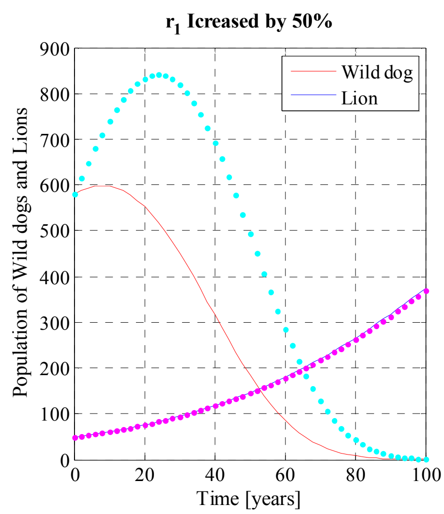

Figure 6. *Changes in the solution of the system (1) – (2) on the effect of increasing the parameter value by 50 percent.*

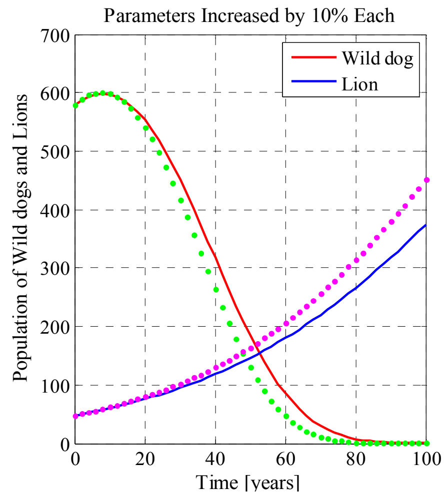

Figure 7. *Changes in the solution of the system (1) – (2) on the effect of increasing parameter values by 10 percent.*

On the other hand, the rest of positive sensitivity indices of the parameters $\alpha_{21}, \eta_1, \alpha_{12}$ and η_2, are lesser compared to the sensitivity index of the parameter delta, δ, by more than 96 percent, therefore when each of the parameter value was increased by 96 percent the changes were difficult to observe. This is shown by Figure 4 and Figure 5, as examples for the rest of the parameters in the group of least positive sensitivity indices.

The parameters r_2, K_2, K_1 and r_1, have a negative sensitivity index. The most negative sensitive parameter is the intrinsic growth rate of wild dog population, r_1, with $X_{r_1}^{R_0} = -0 \cdot 001440884$. If r_1 is increased by 50 percent, then the basic reproduction number R_0 decreases approximately by 33 percent respectively. In this situation the wild dog population increase accordingly and reach its peak in not more than 25 years and start to fall since parameters that hinder the growth of wild dog population are held constant as can be seen in Figure 6.

Figure 7 presents the comparison of wild dog population when the baseline parameters are considered and all the parameters are increased by 10 percent, whereby, the population of wild dog seemed to die out in less than 80 years, this is shown by green dotted line, while the population of lion continued to raise as indicated by purple dotted line.

4. Discussion and Conclusion

4.1. Discussion

A nonlinear mathematical model has been analyzed to study the effects of lions' interference competition on population dynamics of wild dogs. Nevertheless, with the consideration that our research data were estimated, we had to borrow the concept of basic reproduction number $\mathcal{R}_0$, which show that the population of wild dog will survive much longer, that is 80+ years when $\mathcal{R}_0 < 1$, while, when $\mathcal{R}_0 > 1$, the wild dog population will die out in less than 20 years.

Sensitivity analysis shows that, the rate of wild dog mortality caused by lion, $\delta,$ is the most sensitive parameter on $\mathcal{R}_0$, whereby when δ is increased by 50 percent $\mathcal{R}_0$ increases by 49.44 percent appropriately, and the least sensitive is intrinsic growth rate of wild dog population, r_1 which when increased by 50 percent $\mathcal{R}_0$ decreases approximately by 33 percent respectively.

In numerical simulation it is observed that the increase of rate of wild dog mortality caused by lion, tends to decrease the population of wild dogs. But the decrease or absence of wild dog mortality raises the population of wild dog towards its carrying capacity K_1. On the other hand, the indices of least positive sensitive parameter, $\alpha_{21}, \eta_1, \alpha_{12}$ and η_2, and least negative sensitive parameters, r_2, K_2 and K_1 have small influence on $\mathcal{R}_0$ and their changes are not graphically definite. However, the increase of intrinsic growth rate, r_1 while holding other parameters constant, tends to increase the population of wild dog for some years.

This indicate that much work should be on controlling or rather eradicating factors that hinder the growth of wild dog population.

4.2. Conclusion

A competition model for wild dog population dynamics towards interference competition by lions and the effects of human related–mortality was presented, with lion and wild dog populations being variables under consideration. Simulation shows that when the rate of wild dog mortality caused by lion is reduced or eliminated then there will be growth of wild dog population. Moreover, when the rest of parameters are controlled while increasing carrying capacity of wild dog, the intrinsic growth rate of wild dog will be favoured and the population will withstand. This is only possible when protected areas for wild dog population are limited with lion population because the two species, lion and wild dog cannot share the same territory as most of the time the lion species would eliminate or threaten its competitor in resource utilization. On the other hand, human activities that jeopardize lives of wild dogs should be prohibited, that is local people should be stopped from hunting and grazing in the protected areas as well as sport hunting tourism should be abolished and much effort should be on practising sustainable tourism.

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