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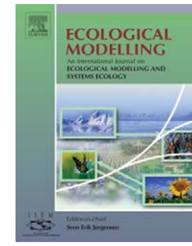

Lion, wildebeest and zebra: A predator–prey model

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ABSTRACT

In this paper, we describe our attempts to fit historical data from the Kruger National Park with a plausible one predator and two mutualistic prey model. Explicit examples of how a model is being developed, improved and tested are rare in literature. This is probably because of the many uncertainties, shortcomings in data, assumptions, speculations and intuitive decisions that form part of the process, which provokes a deep and well-founded fear of the resulting model being criticized. We investigate the effects of including or excluding various phenomena present in population interactions in order to mimic a real world situation. This allows for gaining insight into the behaviour of the system and possible projections of future trends that can be expected. We hope to set a simple yet practical example that may be useful to young researchers and in the educational situation, where computer models are progressively becoming an integral part.

1. Introduction

In the Kruger National Park, South Africa, the central grasslands have supported huge herds of zebra and wildebeest for many years; the lion was and continues to be their principal predator. During the dry period 1969–1972, these grazer species had to be cropped because of over-utilization of vegetation. Zebra were cropped more severely and for a longer period. When cropping was ceased in 1972 after a season of heavy rains, the zebra population declined for a period as expected, and then recovered steadily, while the wildebeest population kept on declining in spite of plentiful graze (Starfield et al., 1976). In this article, we assess what has occurred in the central region of this park after the cropping of wildebeest and zebra was interrupted. Note that no data on the age structure of the species under discussion is available, and the fecundity rates for each age group cannot be deduced from the data. The more widely used discrete approach to modelling population interaction, using difference equations and Leslie matrices, is therefore not suitable in this case. Hence, in our quest to gain insight into what we observe, we use continuous models consisting of differential equations, since population sizes are large enough (generally taken as larger than 1000) to justify a continuous approach.

Predator–prey models (continuous and discrete) have been widely studied in the literature, some of which discuss the effect of mutualism, competition, harvesting and predation in a multi-species system. Recently, for example, Costa et al. (2000) carry out an analysis of both one prey one predator Lotka–Volterra and Leslie–Gower with a weighted escapement harvesting property. A computable general equilibrium approach is developed and applied to model multiple prey and predators in Tschirhart (2004). Features in this model include predators and prey maximizing net energy intake by responding to energy expenditures for capturing prey and no functional response assumptions are made. Gui and Ge (2005) discuss a two species predator–prey model with two life stages, immature and mature, with harvesting of the mature populations. A simulation technique employing statistics and a matrix perturbation analysis called the life-stage simulation analysis is developed in Wisdom et al. (2000) to measure possible effects of uncertainty and variation in rates of population

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growths specifically for purposes of conservation and planning. Other recent literature references include Azar et al. (1995), Dai and Tang (1998), Křivan (1998), Song and Chen (2002), and texts by Jørgenson (1988) and Murray (1993), just to name a few. However, the literature detailing the process of model construction from first assumptions to a final complex model is difficult to find. This paper gives a step-by-step description of the developmental phases for a specific case, which may prove useful to students and others interested in ecological modelling. The interested reader can find a wealth of information by going to the Ecological Modelling web page or using the search engine Science Direct.

To our knowledge there is no recognized three species model that specifically describes interaction between one predator and two mutualistic prey, to which the results of our model could be compared. The challenge therefore is to adapt general theoretical models for multiple species in order to postulate and investigate mathematically the effect of introducing terms that represent various phenomena, such as mutualism, seasonal calving and functional response. We find a reasonable fit to the available data over the period 1972–1987, and apply our newly obtained knowledge to anticipate possible future trends. The models used to describe the population dynamics in this study are extremely simple and conservative, considering all the variables that can have an effect on the dynamics of populations. Nevertheless, they suggest directives for action.

Table 1 – Wildebeest, zebra and lion population densities since 1972

Year	Wildebeest	Zebra
1968	14000	14000
1970	11800	12400
1972	10600	10500
1974	7931	7523
1975	6745[a]	7850
1976	5783	7616
1977	5066	7649
1978	5141	8316
1979	5502	8511
1980	5816	8877
1981	6512	10834
1982	8127	11603
1983	7584	9807[a]
1984	8062	12830
1985	8634	11822
1986	9406	12520
1987	9915	13097
1988	9650	12431
1989	9547	13008
1990	9807	12176
1991	9788	13240
1992	10574	12060
1993	10658	13577
1994	11243	13004

[a] Possible undercounts because of high grass during good seasons.

2. Biological background

The Kruger National Park is situated at the southern end of Africa, on the international border between South Africa and Mozambique. According to Starfield et al. (1976) the central part of the reserve is well suited for various species of grazers and capable of sustaining approximately 12,000 zebra (*Equus burchelli*) and 12,000 wildebeest (*Connochaetes taurinus*). There are various predator species present in Kruger Park, but lion (*Panthera leo*) has the greater impact on the wildebeest and zebra population numbers (Bothma-Du Preez, 1996). In Table 1, population census numbers of wildebeest and zebra are given for the period 1972–1994, while the lion population has been more or less sustained at approximately 300–500 by migrating nomads (Smuts, 1982). The steep decline in wildebeest numbers after cropping was terminated in 1972, and very slow recovery even after 10 years were apparent reasons for concern.

In 1975, a harvesting programme on the lion population was implemented in an effort to allow the wildebeest population to recover. This was discontinued in 1982 after it was realized that nomad lions immigrate to the central parts of the park to replenish the population as soon as zebra and wildebeest numbers picked up (Smuts, 1982).

Two species models describing predator–prey, mutualism or competition situations are well known and are discussed in many texts. For a good mathematical analysis of the continuous approach using systems of differential equations, the reader is referred to Boyce and Diprima (1992) and Murray (1993). Specific deterministic models describing multiple species interaction are not as widely discussed in literature as their stochastic counterparts, although the theory on finding qualitative solutions to two or three species models allows for fruitful investigations in terms of stability. The well-known Lotka–Volterra equations generically expressed by

$$\frac{dX_i}{dt} = X_i\left(b_i + \sum a_{ij}X_j,\right), \quad i, j = 1, 2, \ldots, n$$

lend themselves to be adapted to describe the dynamics of n interacting species in a community. Rates of change in the population size of each of the n species are represented by the equations where b_i describe the intrinsic population growth (in which case the sign of b_i would be positive) or decline (sign of b_i negative) in the absence of the other species, while the signs of a_{ij} would reflect whether species interact in terms of predation, competition or mutualism.

Consider an example where species X_2 predates on species X_1 and X_3, while species X_1 and X_3 are in a mutualistic relationship. A general but very simplistic model for these three species is

$$\frac{dX_1}{dt} = X_1(b_1 - a_{12}X_2 + a_{13}X_3), \quad \frac{dX_2}{dt} = X_2(-b_2 + a_{21}X_1 + a_{23}X_3),$$
$$\frac{dX_3}{dt} = X_3(b_3 - a_{32}X_2 + a_{33}X_3)$$

where the constants a_{ij} and b_i are positive. Modifications may be introduced to this general model in order to describe specific dynamics present in a multi-species community more accurately, for example:

- On first impression it seems that a_{ij} and b_i are all constants, but these parameters could be functions of one or more of the X_i's (Pimm, 1991).