



Structure and sensitivity analysis of individual-based predator–prey models

Muhammad Ali Imron^{a,b,*}, Andre Gergs^c, Uta Berger^b

^a Wildlife Ecology and Management, Faculty of Forestry, Gadjah Mada University, Bulaksumur, Yogyakarta, Indonesia

^b Dresden University of Technology, Faculty of Forest Geo and Hydro-sciences, Piennnerstrasse 8, 01737 Tharandt, Germany

^c RWTH Aachen University, Institute for Environmental Research, Worringer Weg 1, 52074 Aachen, Germany

ARTICLE INFO

Article history:

Received 15 October 2010

Received in revised form

6 April 2011

Accepted 6 July 2011

Available online 23 July 2011

Keywords:

Individual-based model

Ecology

Panthera

Notonecta

Conservation

Population dynamics

Screening design sensitivity analysis

ABSTRACT

The expensive computational cost of sensitivity analyses has hampered the use of these techniques for analysing individual-based models in ecology. A relatively cheap computational cost, referred to as the Morris method, was chosen to assess the relative effects of all parameters on the model's outputs and to gain insights into predator–prey systems. Structure and results of the sensitivity analysis of the Sumatran tiger model – the Panthera Population Persistence (PPP) and the Notonecta foraging model (NFM) – were compared. Both models are based on a general predation cycle and designed to understand the mechanisms behind the predator–prey interaction being considered. However, the models differ significantly in their complexity and the details of the processes involved. In the sensitivity analysis, parameters that directly contribute to the number of prey items killed were found to be most influential. These were the growth rate of prey and the hunting radius of tigers in the PPP model as well as attack rate parameters and encounter distance of backswimmers in the NFM model. Analysis of distances in both of the models revealed further similarities in the sensitivity of the two individual-based models. The findings highlight the applicability and importance of sensitivity analyses in general, and screening design methods in particular, during early development of ecological individual-based models. Comparison of model structures and sensitivity analyses provides a first step for the derivation of general rules in the design of predator–prey models for both practical conservation and conceptual understanding.

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1. Introduction

Predator–prey interaction is one of the classic ecological issues that has been extensively described by mathematical models and increasingly simulated by means of spatially explicit computer models. This interaction is frequently described as numerical responses at the population level and as functional responses at the individual level. For the latter, the Holling Type II function [1] was found to adequately describe empirical observations in many species [2,3], and is most commonly applied in the mathematical description, but also has been adapted to simulation models.

Current developments in individual-based models (IBMs) in ecology have opened new opportunities for testing the suitability of theoretical predator–prey interaction concept for the analysis of natural predator–prey systems and for practical conservation [4–6]. IBMs have frequently been used to understand and predict population dynamics that emerge from individual traits. Examples include the prediction of population dynamics arising from

food availability in water flea [7] or the role of individual home-range maintenance behaviour [8] in the assessment of population persistence of the Iberian lynx [9], tiger [10], and the Florida panther [11] for conservation purpose.

One of the fundamental processes in the development of IBMs is the model analysis. This step involves various approaches and techniques such as the robustness test, statistical analysis, sensitivity analysis, etc. [6]. In spite of the large number of studies employing IBMs for ecological and evolutionary processes that have been published in the last two decades [5], very few have been concerned with evaluating individual-based models by means of sensitivity analyses. In fact, sensitivity analyses might improve ecological models by investigating uncertainties in the parameters, helping us to take inference from the results, to understand the model itself, and to gain insight into the systems represented by the model [6,12].

IBMs sometimes involve many uncertain parameters during model development. To identify those parameters, which will have a major influence on the output of a model, the sensitivity of selected parameters is usually tested using the traditional “one factor at a time” (OAT) method [13]. For example, Karanth and Stith [14] as well as Nilsson [15] tested the effect of prey density and size on the dynamics of predator population or predation

* Corresponding author at: Wildlife Ecology and Management, Faculty of Forestry, Gadjah Mada University, Bulaksumur, Yogyakarta, Indonesia. Tel.: +49 17676398833.
E-mail address: muhammadali.imron@gmail.com (M.A. Imron).

behaviour, while MacCarthy et al. [16] studied the effect of fecundity and the initial number of birds on the population viability of the helmeted honeyeater. A comprehensive sensitivity analysis of all parameters is considered to be a computational process that is not feasible for complex IBMs. Therefore, this kind of analysis is only recommended for relatively simple IBMs [6]. In addition, the use of the sensitivity analysis for IBMs has been neglected due to missing links between the purpose of IBMs and the inferences taken from the results of sensitivity analysis, as well as the usefulness of robustness tests for IBMs [6].

Sensitivity analysis methods vary with different techniques, ranging from local to global and from quantitative to qualitative sensitivity analysis. Among these techniques, screening methods have been recommended to deal with highly complex models [17,12]. In the study presented, the importance of sensitivity analysis as a crucial part in the early development of any ecological individual-based model is addressed. Two predator–prey models of different complexities were chosen in order to derive ecological implications for the particular predator–prey systems, to deduce possible generalisations for the parameterisation of such models and to test the feasibility of two sensitivity analysis methods during the process of IBM development.

2. Model description

The main similarities and differences between the two predator–prey models are described following the ODD (overview, design concepts, and details) protocol as suggested by Grimm et al. [6]. The first example is the Panthera Population Persistence (PPP), a relative complex predator–prey model, describing the population dynamics of Sumatran tigers and their prey [18]. A more detailed description of the PPP model is given in Appendix A.

Table 1

The ranks of the influential parameters in the PPP model after the sensitivity analysis and scoring approach.

Parameter name	Description	Values and units	Ranks
A_{mat}	Maturity age	825 days [24]	28
C_m	Carrying capacity for Red Muntjac	2.2 ind/km ² [25]	5 ^a
C_s	Carrying capacity for Sambar deer	1.4 ind/km ² [25]	4 ^a
G_m	Growth rate of Red Muntjac	2–3 ind/year [26]	8 ^a
G_s	Growth rate of Sambar deer	1 ind/year [27]	13
H_{fem}	Home-range size for female	70 km ² [28]	23
H_{male}	Home-range size for male	116 km ² [28]	14
$H_{t,rad}$	Hunting radius of tigers to detect the presence of prey	1000 m ² (adjusted)	6 ^a
P_c	Probability of successful hunting	50% [29]	2 ^a
P_{preg}	Probability to pregnant	50% (adjusted)	21
T_{fer}	Time duration to switch fertility status	25 days [30]	17
T_{fm}	Time duration to feed Red Muntjac	1–3 days [30,24]	7 ^a
T_{fol}	Time duration for cubs to follow their mother	660 days [30]	1 ^a
T_{fs}	Time duration to feed Sambar deer	7 days [30,24]	12
T_{mate}	Time duration for mating	2 days [30,24]	28
μ_{feed}	Mean rate of movement distance during feeding	400 m/day [10]	9 ^a
μ_{fer}	Mean rate of movement distance during fertile	1000 m/day [10]	19
μ_{hunt}	Mean rate of movement distance during hunting movement	1500 m/day [10]	24
μ_{mat}	Mean rate of movement distance during mating	3000 m/day [10]	10 ^a
μ_{par}	Mean rate of movement distance during parenting	1500 m/day [10]	3 ^a
μ_{preg}	Mean rate of movement distance during pregnancy	2000 m/day [10]	26
μ_{rand}	Mean rate of movement distance during random movement	2000 m/day [10]	11
σ_{feed}	Standard deviation of movement distance during feeding	400 m/day [10]	15
σ_{fer}	Standard deviation of movement distance during fertile	1000 m/day [10]	25
σ_{hunt}	Standard deviation of movement distance during hunting movement	1500 m/day [10]	16
σ_{mat}	Standard deviation of movement distance during mating	1000 m/day [10]	29
σ_{par}	Standard deviation of movement distance during parenting	800 m/day [10]	18
σ_{preg}	Standard deviation of movement distance during pregnancy	1000 m/day [10]	27
σ_{rand}	Standard deviation of movement distance during random movement	2000 m/day [10]	20

The values and units are based on available studies, and if not indicated, adjusted parameters are used.

^a Ten most influential parameters in the PPP model.

The second model is the less complex Notonecta foraging model (NFM), describing the interdependent dynamics of the backswimmers *Notonecta maculata* foraging on their zooplankton prey *Daphnia magna*. The processes, equations, and parameters of the NFM have been published [19,20] and a brief description is also provided in Appendix B.

2.1. Purpose, state variables and scale

The major purpose of the two individual-based models is to understand the potential mechanisms behind the specific predator–prey interaction. Moreover, the PPP model is designed in order to understand the factors determining the population persistence of the Sumatran tiger, using parameterisations of Tesso Nilo national park on Sumatra Island. Based on laboratory studies, the purpose of the backswimmer model is to assess and quantify the role of predators foraging on the population dynamics of the backswimmer *N. maculata* and its zooplankton prey *D. magna*.

Within the two models, all individuals of both predator and prey are characterised by a number of state variables at the start of the simulation. The population dynamics of the Sumatran tiger and two prey species, Sambar deer and Red Muntjac, are simulated in the PPP model. The individuals of Sumatran tiger are differentiated by sex, age, age classes, hunger-level, starvation level, and the reproduction-related status for female tigers. Individuals of Sambar deer and Red Muntjac are differ in age classes. Properties of *N. maculata* are instar, encounter distance as well as attack- and success coefficients. *D. magna* properties are body length and the corresponding size class. The probability of attack and success as well as the time spent handling prey depend on the body length of the encountered daphnid. Brief descriptions of the parameters used in the PPP and NFM are given in Tables 1 and 2, respectively.

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