**Planning the management of wild animal populations using a multi-trophic mechanistic model**

**Context**

Today we will use a simplified version of the model presented in Weclaw (2001) and Weclaw & Hudson (2004).

Weclaw, P. (2001). Modeling the future of woodland caribou in northern Alberta. University of Alberta.

Weclaw, P., & Hudson, R. J. (2004). Simulation of conservation and management of woodland caribou. Ecological Modelling, 177(1-2), 75-94.

This model simulates the population dynamics of caribou, moose and wolves, and the vegetal resources of the two herbivores, i.e. three trophic levels. This system is a typical example of apparent competition: caribou and moose do not consume the same resource, and are therefore not directly competing with each other for resources, but they influence each other through a common predator. Wolves are an opportunist predator, and their favourite prey will change depending on the prey available and their abundance. In Eastern Canada, when white-tailed deers and elks are absent, moose are their main prey. They will nonetheless also feed on caribou.

Woodland caribou (*Rangifer tarandus caribou*) do not migrate, and avoid predation by selecting old conifer forest patches, where they eat some plants and terrestrial or arboreal lichen, away from younger deciduous and mixed forest patches where moose feed. However, human activities such as logging activities increase the proportion of deciduous trees (which come before conifer forest in the forest succession stages), and therefore increase moose populations, which in turn will lead to increases in wolf populations, increasing predation pressure on caribou.

Here we will simulate such a system, and explore different management options.

**Model description**

The original model by Weclaw (2001) and Weclaw & Hudson (2004) is a bit too complex for this practical, so we will limit it to the following elements (within the red shape):

A diagram of a plant

Description automatically generated

During this practical, you will implement a **discrete**, mechanistic model for six distinct populations: lichen, plants, moose forage, caribou, moose and wolves.

**First trophic level – producers**

* Lichen, plant and moose forage growth are based on a typical logistic growth, in which birth is provided by the following equations:

Where

L(t) ≡ lichen biomass density available (kg/ha) at time t

sL ≡ lichen annual max growth potential (unit-less)

KL ≡ lichen carrying capacity (kg/ha)

P(t) ≡ plant biomass density available (kg/ha) at time t

sP ≡ plant annual max growth potential (unit-less)

KP ≡ plant carrying capacity (kg/ha)

H(t) ≡ moose forage biomass density available (kg/ha) at time t

sH ≡ forage annual max growth potential (unit-less)

KH ≡ forage carrying capacity (kg/ha)

* Lichen, plant and moose forage are depleted through herbivory following a type II functional response. Death is therefore provided by the following equations:

Where

C(t) ≡ caribou density (animal/ha)

lL ≡ annual lichen requirement by an individual caribou (kg)

hL ≡ maximum rate of lichen intake (kg/ha)

lP ≡ annual plant requirement by an individual caribou (kg)

hP ≡ maximum rate of plant intake (kg/ha)

M(t) ≡ moose density (animal/ha)

LH ≡ annual forage requirement by an individual moose (kg)

HH ≡ maximum rate of moose forage intake (kg/ha)

* Lichen, plant and forage populations are therefore determined by the following equations:

**Second trophic level – primary consumers**

* Caribou and moose growth are based on type II functional response, which depends on forage availability

Where

fC ≡ maximum fecundity for caribou (average number of offspring per individual)

You also need an equation for moose. In the model, there is only one type resource for moose, so you only need one fraction in the equation instead of two. And you will all need the new parameter:

fM ≡ maximum fecundity for moose (average number of offspring per individual)

* Caribou and moose die when there is not enough food to sustain the whole population

As for growth, you also need an equation for moose, and you only need one fraction to account for the fact that there is only one type of resource.

* Caribou and moose also die from predation by wolves

Where

W(t) ≡ wolf density (animal/ha)

eC ≡ asymptotic kill rate on caribou per wolf (unit-less)

dC ≡ predation efficiency on caribou (animal/ha; prey density at half the asymptotic kill rate)

eM ≡ asymptotic kill rate on moose (animal/ha)

dM ≡ predation efficiency on moose (animal/ha; prey density at half the asymptotic kill rate)

* Caribou and moose populations are therefore determined by the following equations:

**Third trophic level – secondary consumers**

* Wolf growth is based on type II functional response, which depends on caribou and moose availability

Where

b ≡ upper limit of annual rate of increase (unit-less)

* Wolves die naturally at a constant rate

Where

g ≡ wolf death rate (unit-less)

* Wolf population is therefore determined by the following equation:

We need the values of all our parameters:

|  |  |  |
| --- | --- | --- |
| Parameter | Description | Value |
| sL | lichen annual max growth potential (unit-less) | 0.07 |
| sP | plant annual max growth potential (unit-less) | 0.5 |
| sH | forage annual max growth potential (unit-less) | 0.5 |
| KL | lichen carrying capacity (kg/ha) | 870 |
| KP | plant carrying capacity (kg/ha) | 240 |
| KH | forage carrying capacity (kg/ha) | 970 |
| lL | annual lichen requirement by an individual caribou (kg) | 2.68275 |
| lP | annual plant requirement by an individual caribou (kg) | 2.68275 |
| lH | annual forage requirement by an individual moose (kg) | 3.1682 |
| hL | maximum rate of lichen intake (kg/ha) | 400 |
| hP | maximum rate of plant intake (kg/ha) | 300 |
| hH | maximum rate of moose forage intake (kg/ha) | 1000 |
| fC | maximum fecundity for caribou (average number of offspring per individual) | 1 |
| fM | maximum fecundity for moose (average number of offspring per individual) | 1.5 |
| eC | asymptotic kill rate on caribou per wolf (unit-less) | 1.85 |
| eM | asymptotic kill rate on moose (animal/ha) | 0.6 |
| dC | predation efficiency on caribou (animal/ha; prey density at half the asymptotic kill rate) | 460 |
| dM | predation efficiency on moose (animal/ha; prey density at half the asymptotic kill rate) | 46 |
| b | upper limit of annual rate of increase (unit-less) | 0.8 |
| g | wolf death rate (unit-less) | 0.38 |
| mM | Hunting rate on moose (see end of practical) | 0 |
| mW | Hunting rate on wolf (see end of practical) | 0 |

And we also need the initial value of the six variables at time t=0:

|  |  |  |
| --- | --- | --- |
| Variable | Description | Initial conditions |
| L(t) | lichen biomass density (kg/ha) | 870 |
| P(t) | plant biomass density (kg/ha) | 240 |
| H(t) | moose forage biomass density (kg/ha) | 970 |
| C(t) | caribou density (animals/ha) | 7 |
| M(t) | caribou density (animals/ha) | 25 |
| W(t) | caribou density (animals/ha) | 8 |

**TO DO**

**Check the equations**

One important thing when designing such a model with multiple equations is to make sure all our equations are balanced. That is, the units on each side of the “=” sign are the same. For example, if I have a weight (kg) on the left hand side of an equation, and a product of a density (kg/ha) and an area (ha) on the right-hand side, my equation is balanced:

kg = (kg/ha) × ha

For the equations above, check that they are indeed balanced (do it for a couple of equations). If you have a doubt about the definitions, you can go to the original article and thesis, which I uploaded on Learn.

**Base-model in R**

I uploaded a skeleton of the script you can fill with the equations above (i.e. (lichens, plants, forage, caribou, moose and wolves). If this is too much, I also uploaded the full script, but try to write a couple of equations at least.

First, set the animal initial populations to 0, and run the model. What happens? Discuss with your neighbour(s).

Then, set the caribou and moose initial populations to the values in the table above. How are the two species doing?

Finally, set the wolf initial population to the value in the table above. What happens to the moose and caribou populations? Which one is more impacted?

**Let’s test different conditions and management options**

* Let’s assume we implement some management action that limits the number of wolves to 10 individuals/ha maximum. Implement this in your model (hint: you need to use the function min() when computing the value of W[t]). What happens to the model outputs? Explain the new behaviour.
* We will now implement a similar management action, but this time by limiting the number of moose to 30 individuals/ha maximum. Implement this in your model (hint: you need to use the function min()on a different line of code). What happens to the model outputs? Explain the new behaviour.
* Since it is hard and costly to know exactly how many individuals there are in a population and to keep animal density at a given value, managers decided to promote wolf hunting instead. We will assume that the number of wolves killed each year is a proportion of the total number of wolves. This can be described by the following equation:  
    
     
  where mW is the proportion of wolves killed, which we set to 0.1. Modify your code to add this element to the computation of W[t]. What happens to the model outputs? Explain the new behaviour.
* As before, we can decide to implement hunting on the moose population instead of the predator. This may be considered more ethical since the meat can be used for food, and herbivore populations usually take more time to recover than predator populations. Moose hunting can be described by the following equation:  
    
     
  where mM is the proportion of moose killed, which we set to 0.1. What happens to the model outputs? Explain the new behaviour.
* Finally, based on this model, which recommendation would you make to manage the system (also consider a laissez-faire scenario when no management is implemented)?

**Additional tasks**

* Implement hunting, but only every 10 years, which may be easier to implement as a management action than every year. How does it change the model behaviour?
* As mentioned above, logging activities increase the proportion of deciduous trees, where moose find their forage, at the expanse of conifer forests where caribou find theirs. How would you include this aspect in your model (hint: you need to change three parameter values)? How do these changes impact the outputs?
* Explore management options under such logging activities. Would you still make the same recommendations?