SCAVCOMP-ABM

Scavenging and competition for carrion ABM v40.2

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ODD Protocol

This model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual- and agent-based models (Grimm et al., 2010). The model has been implemented in NetLogo 6.2.2 (Wilensky, 1999).

1. Purpose

The SCAVCOMP-ABM model simulates the competition for carrion among hominins and carnivores in an Early Pleistocene European ecosystem. It is designed to evaluate the viability of scavenging as a foraging strategy for hominins under different compositions of the carnivore guild and different group sizes.

2. Entities, state variables, and scales

The environment of the model consists of a grid of cells, which we refer to as "patches". We refer to the mobile entities as "agents". Agents represent hominin groups and carnivore packs. There are 8 different types of carnivore packs that represent 8 different species from the late Early Pleistocene of Europe (1.4-0.8 Ma). Moreover, agents are classified in three different foraging types: "scavengers", "predators" and "hybrids". Each foraging type is defined by a different set of state variables.

The state variables of the environment are listed and described in Table 1, the state variables of the agents are described in Table 2. We follow the terminology of Montgomery (2013) where the parameters, which may be changed between simulation experiments are called "factors", the factor values are called "levels", parameters that are fixed are called "constants", and the output variables are called "responses".

Table 1. State variables of the patches.

Name	Type	Description
available-carrion-units	response	Amount of carrion resources in the patch. Measured in kcal.
pcolor	response	built-in NetLogo variable which holds the color of the patch, which is determined by available-carrion-units.
plabel	factor	built-in NetLogo variable which holds the label text of the patch; not used in the present model
plabel-color	factor	built-in NetLogo variable which holds the color of the label of the patch; not used in the present model
pxcor	response	built-in NetLogo variable which holds the x-position of the patch on the map
pycor	response	built-in NetLogo variable which holds the y-position of the patch on the map

Table 2. State variables of the agents

Name	Type	Description
bmr	factor	Only scavengers and hybrids. Basal metabolic rate of an individual in kcal.
breed	constant	built-in NetLogo variable which holds the breed of the agent. Values “hominins”, “p_brevirostris”, “homotherium”, “megantereon”, “panthera”, “puma”, “lycaon”, “canis_etruscus”, ”crocuta_crocuta”.
carrion-units-from-prey	factor	Only predators. Amount of energy contained in a carcass produced by the agent.
carrion-units-production-rate-per-hour	factor	Only predators. Probability that the agent will produce a carcass during a tick (1 hour).
collected-carrion-units	response	Only scavengers and hybrids. Sum of the amount of energy, in kcal, gained by an agent in every tick.
color	constant	built-in NetLogo variable which holds the color of the agent.
der	factor	Only scavengers and hybrids. Daily energy requirements of an individual in kcal.
energy	response	Only scavengers and hybrids. Current energy in kcal.
foraging-type	constant	All agents. Type of foraging behaviour: “scavenger”, “predator” or “hybrid”.
heading	response	built-in NetLogo variable which holds the direction of movement of the agent.
hidden?	constant	built-in NetLogo variable which allows switching the visualization of agents on or off; hidden? = False (agents are visible).
hunger-value	constant	Only scavengers and hybrids. Energy limit, in kcal, to search for food.

Name	Type	Description
hungry	response	Only scavengers and hybrids. *Hungry* = ”True” If *energy* < *hunger-value*; else *hungry* = “False”
initial-density-canis_etruscus	factor	Initial number of *Canis etruscus* individuals per km^2
Initial-density-crocuta_crocuta	factor	Initial number of *Crocuta crocuta* individuals per km^2
initial-density-hominins	factor	Initial number of hominin individuals per km^2
initial-density-homotherium	factor	Initial number of *Homotherium latidens* individuals per km^2
Initial-density-lycaon	factor	Initial number of *Lycaon lycaonoides* individuals per km^2
Initial-density-meganthereon	factor	Initial number of *Meganthereon cultridens* individuals per km^2
Initial-density-p_brevirostris	factor	Initial number of *Pachycrocuta brevirostris* individuals per km^2
initial-density-panthera	factor	Initial number of *Panthera gombaszoegensis* individuals per km^2
initial-density-puma	factor	Initial number of *Puma pardoides* individuals per km^2
last-actual-carrion-units-from-prey	response	Only predators. Amount of carrion (kcal) produced by the agent in the current tick.
last-energy-gain	response	Only scavengers and hybrids. Amount of energy (kcal) obtained by the agent in the current tick.
movement	response	Only scavengers and hybrids. Movement “on” or “off”.
pack-size	factor	All agents. Number of individuals in the pack.
produced-carrion-units	response	Only predators. Sum of the amount of carrion (kcal) produced by the agent in every tick
range-of-view	factor	Only scavengers and hybrids. Distance (km) from which an agent may perceive that a patch contains carrion.
rank	factor	All agents. The rank determines the behaviour of the agent when there are more than one agent in the patch.
shape	constant	built-in NetLogo variable which holds the shape of the agent. Values “hyaena”, “wolf” or “hominin”.
size	constant	built-in NetLogo variable which holds the size of the graphical representation of the agent.
velocity	factor	Only scavengers and hybrids. Movement speed in km/h.
who	response	built-in NetLogo variable which holds the ID of the agent.
xcor	response	built-in NetLogo variable which holds the x-position of the agent on the map.
ycor	response	built-in NetLogo variable which holds the y-position of the agent on the map.

A patch represents 1 km^2 of real space. The size of the “world“ is 51 x 51 patches and represents an area of 2,601 km^2. We refer to a time step as a “*tick*“, and it represents 1 hour of real time. Simulations were run for 9,000 hours (375 days).

3. Process overview and scheduling

Each tick starts with the carrion-wastage submodel and continues with the move-predators and then the move-scavengers-and-hybrids submodels. Agents move one after another, sort in a random order. After all scavengers and hybrids moved, hybrid and scavenger agents collect-carrion-or starve in random order and, once all them finished, the produce-carrion submodel starts. Predators also produce-carrion in a sequential and random order.

State variables are updated asynchronously, i.e. they are immediately assigned a new value as soon as that value is calculated by a process.

4. Design concepts

Basic principles

The environment of the model is a homogeneous landscape were a hominin population and a guild of large carnivores are represented. Agents represent a "pack" or "group" of individuals of the same species. Solitary species have *pack-size* = 1. The model allows to compose the carnivore guild by selecting species from the pool of eight species present in the European late Early Pleistocene (Rodríguez, 2017; Rodríguez et al., 2012). Carnivores are classified as predators, scavengers or hybrids. Hominins are scavengers. Each predator species produces discrete units of carrion (carcasses) of different size and at a different rate. The size of the carcass and the rate of production depends on the size of the preferred prey and the size and ethology of the predator species. Scavengers actively search for carrion and consume it to obtain energy to replace the energy spent. Scavengers spend energy when they are quiet at a lower rate than when they are moving. Scavengers die when their *energy* drops to zero. Since agents represent packs or groups in social species, all the individuals in the group die at the same time when energy drops to zero. The model assumes that social species distribute energetic resources equally among their members, even if resources are scarce. This is a simplification of the model, unrealistic in the real world. Agents do not reproduce, because the model is intended to simulate a single annual cycle. Predators do not die. Some carnivore species are considered "hybrids". A hybrid is a carnivore that kills prey, as predators do, but it also feeds on the carcasses produced by other carnivores. Hybrids obtain part of their energy requirements from carcasses produced by predators, and in doing so they behave as scavengers.

The model is intended to show the effect of the size of the foraging group, the composition of the carnivore guild, and the productivity of the environment on the performance of Early Pleistocene hominins as scavengers and the interaction between these factors. The productivity of the environment is represented in the model by the value of the initial density of each predator species, since it is assumed that more productive ecosystems can sustain higher populations of predators (Rodríguez and Mateos, 2018).

Emergence

The population size of each scavenger at the end of the simulation run is equal or lower than its initial population. The variations in population size are due to the death of agents by starvation. In order to survive to the end of the simulation, each agent should balance its energy expenditure and energy gain. The cost of survival is measured as the total energy gained by the agent throughout the simulation run. The ability of a scavenger to accrue energy (eat carrion) is proportional to its *pack-size,* because agents with a larger *pack-size* have a higher *rank* and displace lower-ranked agents. However, a larger pack requires more energy, and energy is a resource distributed in discrete units (carcasses), which size and abundance depend on the composition of the carnivore guild. Thus, cost of survival and survival probability are determined by the complex interaction of the *pack-size* of the agents; the size of carcasses, which in turn depends on the composition of the carnivore guild; and the abundance of carcasses, which depends on the composition of the carnivore guild and the abundance of predators, determined by their initial density.

Adaptation

Scavengers turn *hungry* when their *energy* is lower than the *hunger-value.* If there is carrion in their patch when they are hungry, they stay in the patch and eat; otherwise they move to the nearest cell containing carrion within its *range-of-view*. If they are not *hungry* they stay in the patch, saving energy, but if there is a predator or other scavenger with a higher *rank* located in the same patch they move away.

Objectives

Scavengers aim to maintain their energy balance either by not moving, when not hungry or by moving to find carrion and refill their energy.

Learning

Learning is not included in the model.

Prediction

The agents have not prediction capability.

Sensing

Scavengers and hybrids are able to monitor their own *hungry* value to determine whether they should eat or not. They also know the *available-carrion-units* in the patches inside their *range-of-view*. Moreover, all agents are able to know the *rank* of the other agents in the same patch.

Interaction

There is an indirect interaction among scavengers and hybrids, since they compete with other scavengers and hybrids for carrion. There are also direct interactions among agents determined by their rank. When one or more agents coincide in the same patch, only the agent with the highest rank stays in the patch. The rest of agents move away.

Stochasticity

Predators move randomly and produce carrion at every tick with a probability determined by their *carrion-units-production-rate-per-hour*. Thus, the location and time of appearance of a new carcass in the environment is a stochastic process. When scavengers are *hungry* and there are no patches with *available-carrion-units* > 0 at a distance smaller or equal to their range-of-view, they move at random.

When two or more agents of the same rank coincide in the same patch, the agent that stays in the patch or collects carrion is selected at random.

Collectives

Agents belong to different species. All the agents of the same species have the same values for the state variables that define a species. A species is defined by a different set of state variables for scavengers, predators and hybrids. Scavenger species are defined by *pack-size, foraging-type, der, bmr, energy-limit, rank, velocity, initial-density, color*. Predator species are defined by *pack-size, foraging-type, initial-density, shape, size, breed, carrion-units-production-rate-per-hour, carrion-units-from-prey*. Hybrids are defined by the two sets of state variables listed above.

Observation

The model allows for various analyses of responses (Table 3). These responses are measured at each tick.

Table 3. Model responses

Name	**Description**
total-uncollected-carrion-units	Total amount of carrion currently available across all patches. Measured in kcal.
total-collected-carrion-units	Total amount of carrion collected by hybrids and scavengers during the current tick. Measured in kcal.
total-carrion-units-production	Total amount of carrion produced by predators and hybrids from the start to the current tick. Measured in kcal.
collected-carrion-units-by-hominins	Total amount of energy collected by all hominin agents from the start to the current tick. Measured in kcal.
collected-carrion-units-by-p_brevirostris	Total amount of energy collected by all *p_ brevirostris* agents from the start to the current tick. Measured in kcal.
collected-carrion-units-by-canis_etruscus	Total amount of energy collected by all *canis_etruscus* agents from the start to the current tick. Measured in kcal.
collected-carrion-units-by-crocuta_crocuta	Total amount of energy collected by all *crocuta_crocuta* agents from the start to the current tick. Measured in kcal.
energy-spent-by-hominin-pack	Average amount of energy spent by one of the surviving hominin agents from the start to the current tick. Measured in kcal.
energy-spent-by-p_brevirostris-pack	Average amount of energy spent by one of the surviving *p_brevirostris* agents from the start to the current tick. Measured in kcal.

Name	**Description**
energy-gained-by-hominin-pack	Average amount of energy obtained by one of the surviving hominin agents from the start to the current tick. Measured in kcal.
energy-gained-by-p_brevirostris-pack	Average amount of energy obtained by one of the surviving *p_brevirostris* agents from the start to the current tick. Measured in kcal.
produced-carrion-units-by-homotherium	Total amount of carrion produced by *homotherium* agents from the start to the current tick. Measured in kcal.
produced-carrion-units-by-megantereon	Total amount of carrion produced by *meganthereon* agents from the start to the current tick. Measured in kcal.
produced-carrion-units-by-panthera	Total amount of carrion produced by *panthera* agents from the start to the current tick. Measured in kcal.
produced-carrion-units-by-lycaon	Total amount of carrion produced by *lycaon* agents from the start to the current tick. Measured in kcal.
produced-carrion-units-by-canis_etruscus	Total amount of carrion produced by *canis_etruscus* agents from the start to the current tick. Measured in kcal.
produced-carrion-units-by-crocuta_crocuta	Total amount of carrion produced by *crocuta_crocuta* agents from the start to the current tick. Measured in kcal.
max-available-carrion-units	Maximum energy available in a patch during the current tick. Measured in kcal.
number-of-encounters-with-hyaenas	Counts the times a *hominin* agent is located in the same patch than a *p-brevirostris* agent if the rank of *p-brevirostris* is higher than the rank of *hominin.* Represents the number of times a hominin pack is chased away by a *p-brevirostris.*
number-of-encounters-with-predators	Counts the times a *hominin* agent is located in the same patch than a *predator* agent of higher rank than itself. Represents the number of times a hominin pack is chased away by a *predator*.
number-of-encounters-with-competitors	Counts the times a *hominin* agent is located in the same patch than another scavenger (including other hominin) or a hybrid and moves away. Represents the number of times a hominin pack loses the competition to stay in the patch.

5. Initialization

The initial values of several state variables may vary among simulations. Most of them should be set by the researcher based on the current knowledge on the biology of the species included in the model, general ecological principles, or the specific hypothesis to be tested. The duration of the simulation is determined by the factor *stop-at-hours-value* if the factor *stop-at-hours* is “on“. If the factor *stop-at-no-more-scavengers* is “on“ the simulation stops when all scavengers die.

The initial density of each species should be set to represent the productivity of the environment (assuming more productive environments support higher population densities). Species excluded from the carnivore guild in the simulation are determined by *initial-density* = 0.

Agent types (species) with an initial density equal to zero are excluded from the simulation. Each scavenger and hybrid are created with a random value of *energy*, within the limits determined by the selected option for *initial-nutrition-state.*

If *initial-nutrition-state* is set as “bad condition” *energy* is set at the *bmr* increased in a random quantity between zero and 33% of the *energy-limit.*

If *initial-nutrition-state* is set as “middle condition” *energy* is set at a random value between 33% and 66% of the *energy-limit.*

If *initial-nutrition-state* is set as “good condition” *energy* is set at a random value between 66% and 99% of the *energy-limit.*

If *initial-nutrition-state* is set as “random” *energy* is set at a random value between *bmr* and the *energy-limit.*

The *energy-limit* is computed as: *energy-limit* = 3 × *der* × *pack-size*

Carrion is created in every patch at random, with the probability established by the *initial-carrion-probability* factor. It is also possible to establish a delay in the time scavengers appear in the landscape. This delay is determined by the *hours-without-scavengers* factor and it is intended to prevent all scavengers to die of starvation during the first ticks of the simulation due to scarcity of carrion.

The *daily-carrion-wastage-rate* (kcal/day) factor should be set to determine the rate of decay of the *available-carrion-units* present in the patches.

The *rank* of all predators and *crocuta_crocuta* is 5, and the *rank* of *canis_etruscus* is 1. The ranks of *hominins* and *p_brevirostris* are determined as:

p_brevirostris rank = pack-size-p_brevirostris × 2.5

hominins rank = pack-size-hominins / 2

Thus, a solitary *p_brevirostris* has a lower *rank* than any predator, but higher than *canis_etruscus* and a group of hominins with less than 5 individuals. A group of six or more hominids has a rank higher than any other agent. These values are arbitrary, but they reflect the effect of group size on the confrontation between hominins and carnivores.

The following factors defining the different species may be changed among simulations: *pack-size, der, bmr, velocity, carrion-units-production-rate-per-hour, carrion-units-from-prey*. The *energy-limit* is set as three times the daily energy requirements (*der*) multiplied by *pack-size*, and *hunger-value* is set at half the daily energy requirements multiplied by *pack-size*.

6. Input data

The model does not use input data to represent time-varying processes.

7. Submodels

Carrion-wastage

The *carrion-wastage-rate-per-hour* is computed dividing *daily-carrion-wastage-rate* by 24 hours. Then, *carrion-wastage-rate-per-hour* is subtracted from the *available-carrion-units* in all the patches with *available-carrion-units* > 0. In the patches where the obtained value is lower than 0 *available-carrion-units* is set to 0

Carrion wastage simulates the "natural decay" of the energetic content of a carcass abandoned in the landscape. Decay occurs by the action of microorganisms, but also because the carcass is consumed by other species not simulated in the model (birds, invertebrates, small carnivores, etc.).

Move-predators

Agents with *foraging-type* equal to "predator" are asked to move randomly around the environment at the speed determined by their *velocity.*

The random movement of predators makes the selection of patches where a new carcass will appear a stochastic process.

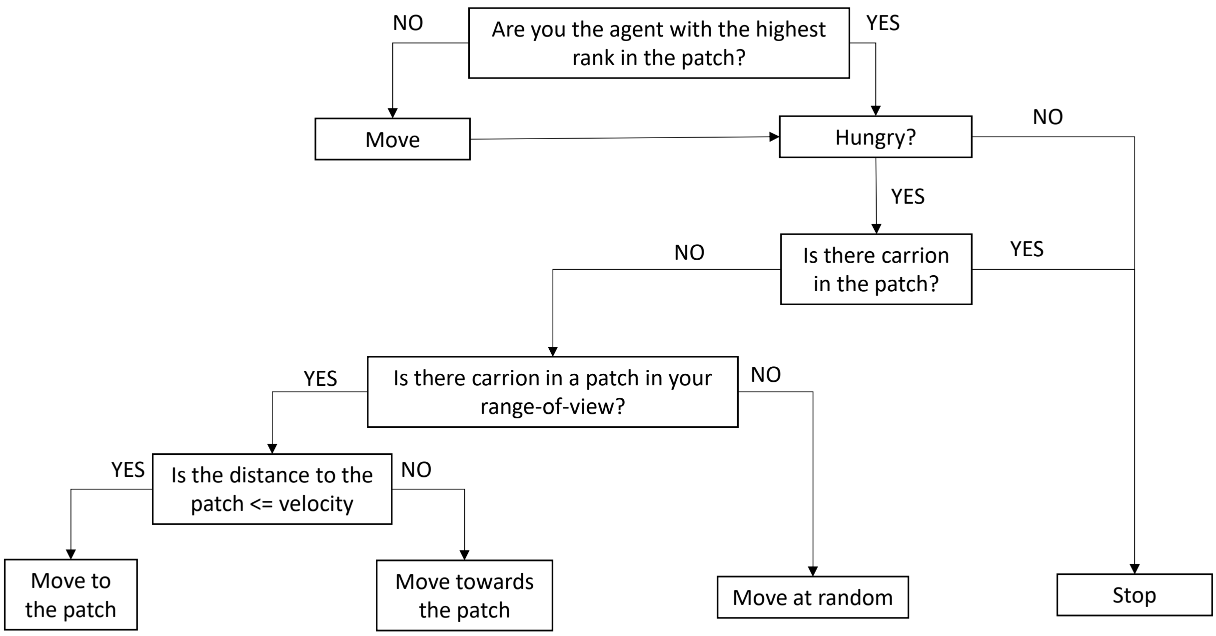
Move-scavengers-and-hybrids

This procedure affects all agents with *foraging-type* equal to "scavenger" or "hybrid" and is summarized in Figure 1. As a first step, the *rank* of all the agents (scavengers, hybrids and predators) present in patches where there is more than one agent is determined. All agents other than the one with the highest rank turn 180 degrees and move away at a speed determined by its velocity. If there are more than one agent in the patch with the highest rank, the agent that stays in the patch is selected at random among them.

After this, scavengers and hybrids check the existence of carrion in the patch they are and proceed as follows. If there is carrion in the patch where a scavenger or hybrid agent is (*available-carrion-units* > 0), it stays in the patch. If *available-carrion-units* = 0 and the agent is not *hungry,* it stays in the patch. If there is no carrion in the patch and the agent is *hungry* it moves towards the nearest patch with carrion inside its *range-of-view*. If there are no patches with carrion in its *range-of-view*, it moves in a random direction.

Direct competition for a single carcass among two agents is simulated by allowing only one of them to stay in the patch containing carrion. Moreover, it is assumed that scavengers avoid direct interaction with predators unless the scavenger is able to chase away the predator (the predator has a lower *rank*). However, note that the model does not intend to simulate kleptoparasitism or confrontational scavenging (Bunn, 2001; Domínguez-Rodrigo, 2002; Pobiner, 2020). Scavengers and hybrids tend to save energy. Thus, they only move when they are hungry and there is not carrion in the patch. The hungry agent stays in the patch even if *available-carrion-units* are close to 0. This is against the predictions of the Optimal Patch-Use Models developed in the frame of the Optimal Foraging Theory (MacArthur and Pianka, 1966; Winterhalder and Smith, 2000, and references therein), and it is assumed to be a simplification of the model. Future versions of SCAVCOMP-ABM may consider to incorporate an Optimal Patch-Use Model to simulate the behaviour of the foraging scavengers.

Figure 1. Flow chart of the move-scavengers-and-hybrids submodel.



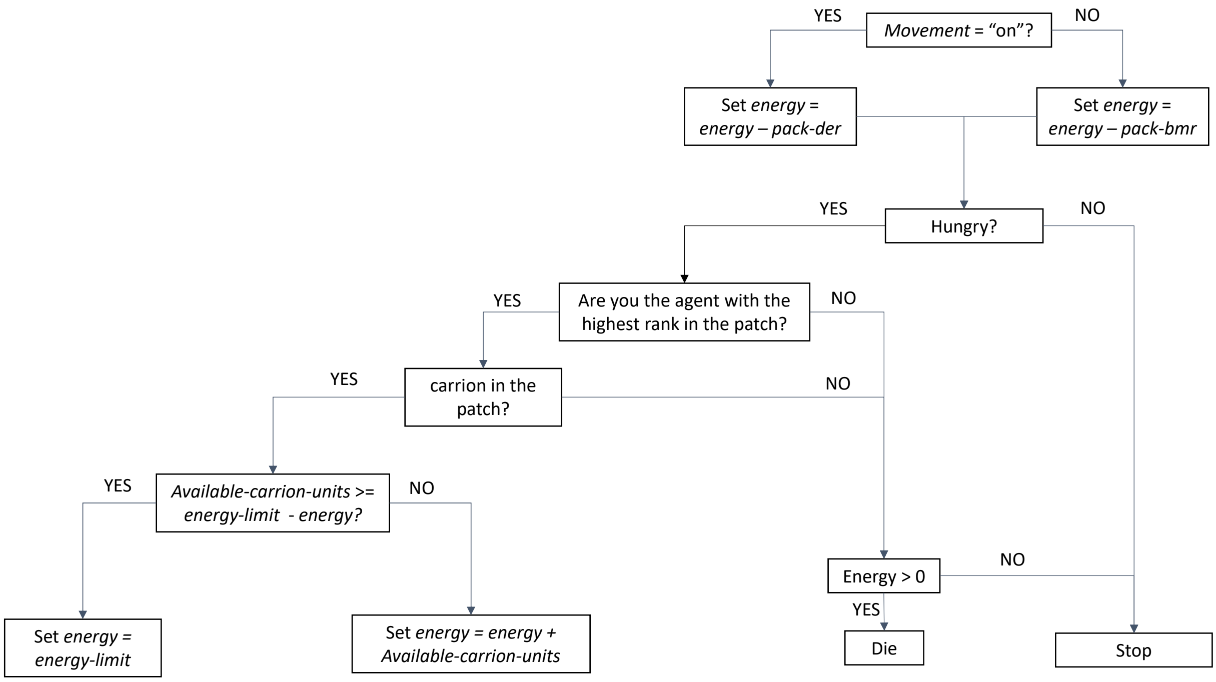
Collect-carrion-or-starve

The energetic expenditure of each scavenger and hybrid during the current tick is computed (Figure 2). If the agent moved during the current tick energy expenditure is determined by its *pack-der (Pack-der= der* × *pack-size*), otherwise energy expenditure is determined by its *pack-bmr (Pack-bmr= der* × *pack-size).*

In the next step hungry agents collect carrion if it is available in the patch they are, but only if they are the agent with the highest rank in the patch (Figure 2). Agents collect the amount of carrion (kcal) necessary to rise their *energy* value to their *energy-limit,* or all the *available-carrion-units* if there is not enough carrion in the patch to reach their *energy-limit.* The *hungry* state variable of the agent is eventually updated. Scavengers that spent all their energetic reserves (*energy* <=0) die. The carrion content of the patch *(available-carrion-units)* is diminished in the quantity collected by the agent.

Some of the agents that moved during the current tick to avoid agents with a higher rank, or because they were hungry and there was not carrion in their patch, may arrive to a patch with carrion were there are other agents. Thus, it is necessary to introduce the condition that only the agent with the highest rank in the patch may consume carrion.

Figure 2. Flow chart of the collect-carrion-or-starve submodel.



Produce-carrion submodel

Predators produce carrion sequentially and stochastically in the patch where they are, with a probability determined by their *carrion-production-rate-per-hour* and a quantity determined by their *carrion-units from-prey*. The carrion content of the patches is updated.

The carrion production process is an oversimplification of the model because the focus is on carrion consumption, not in carrion production. In the real world large carnivores kill a prey every few days (Sunquist and Sunquist, 2009), and may feed on the carcass for several days before it is abandoned (Gidna et al., 2014).

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