Documentation for MO*Ov*POP

Purpose

MO*Ov*POP is designed to simulate population dynamics of white-tailed deer and generate pre-harvest deer population (abundance, sex-age composition and distribution in the landscape) for the selected sampling region. These population data are stored as an Excel file.

Entities, state variables and scales

Spatial scales: MO*Ov*POP landscape can be set up for individual counties as well as for current or potential CWD management zones. Miles (rather than kilometers) are used as a distance and area measure in this work because of the past and current norms of the region and its management agencies, and the related need to make the results immediately applicable to those same agencies

Temporal scale: MO*Ov*POP has a monthly time step, and duration of the simulation is 25 years.

Entities: MO*Ov*POP has two entities: patches and deer. Irrespective of the region selected for simulation, each patch in the model landscape represents one square mile. Deer are modeled as individuals occupying the patches.

State variables: Each patch is characterized by its percent forest cover (*forest-percent*), whether it is a border or non-border patch (*border*), whether it qualifies as a deer habitat (*dh*), deer occupancy (*do*), and mean forest-percent (*dfp*). The mean forest-percent is calculated for each patch by averaging forest cover of a patch and its immediate neighbors. Each deer has eight state variables, which define individual characteristics like age, sex, group membership and status (Table 1).

Process overview and scheduling

Processes: Processes included in this model are all related to deer: individual growth, male and female yearling dispersal, bachelor group formation, doe social group formation, fawning, hunting and non-hunting mortality. A doe social group is comprised of an adult doe (group leader) with several generations of her female offspring, while bachelor group is an aggregation of nonrelated adult males outside the breeding season[1]. To model group dynamics, one adult member of each doe social group and bachelor group was designated as leader.

Schedule: Growth (increase age by one month) of individuals is scheduled at the beginning of the time step, and is followed by non-hunting mortality. Processes like dispersal (male yearling/female yearling), group formation (bachelor group/ doe social group), and hunting mortality which only occur during a specific time-step (month) are executed after deer-growth and non-hunting mortality. In the fifth month every year, male and female yearling dispersal is scheduled before fawning. Observer actions (census and plotting graphs) are scheduled at the end of the time step. The month counter resets after every 12 months.

Design concepts

Basic principles.

Processes like social organization, group dynamics, dispersal, and hunting mortality occur at an individual level and influence interactions among individuals. Such interactions underpin host heterogeneity, and thereby influence disease transmission in a host population. We incorporated these processes in the basic model so that the model-generated population reflects heterogeneity observed in real-world host populations. MO*Ov*POP-generated deer population can be used to initialize MO*Ov*CWD (model simulating CWD transmission dynamics in deer population) and MO*Ov*POP*surveillance*.

Emergence. Age and sex structure of the model deer population, as well as the deer distribution pattern, emerge from the model.

Adaptation: Adaptation is modeled in MO*Ov*POP in two processes, male dispersal and female group dynamics. Male fawn and yearling dispersal distances are based on percent forest cover of the individual's home range [2,3]. Female group size dynamics adapts to the current group size and membership. Processes like group-fission and new group formations are based on current group size, and occur around fawning season.

Sensing: Agents (deer) are modeled to 'sense' their environment (patch variables or state variables of other agents) before making some behavioral decisions. Male yearling deer 'sense' the percent forest cover of their home range and determine dispersal distance. Doe social group members can sense current group size, group leaders can sense solitary female deer on their patch, and solitary female deer are aware of the number of doe social groups and group leaders in their neighborhood (own patch and eight neighboring patches, nine square mile area).

Interaction: Deer group dynamics and sociality is included in this model to implicitly simulate within- and between- group interactions in the deer population.

Stochasticity: Deer mortality rates (natural and hunting) are deterministic, but individuals that die during a time step are chosen randomly. Male and female group leaders are selected randomly from a set of potential candidates.

Observation: MO*Ov*POP has a graphical display of deer occurring on the landscape, and their abundance and distribution are updated as the model executes. Another graphical display plots deer abundance versus time, and monitors display number of deer in each age-sex-class. Additionally, pre-harvest and post-harvest population abundance by sex-age-class is recorded in the output file *DeerPopDy* for each year of model run. Just before the hunting season in the last year of simulation, the values of all deer and patch variables are written to a file (*DeerPopulation*). This file can be used to initialize model extensions.

Initialization

At initialization of MO*Ov*POP, the user must select and load a GIS file for the desired sampling region. For Missouri, forest cover data (United States Geological Survey 1992 National Land Cover Data) for each sampling region has been converted to a forest percentage grid of 1 square mile patches to facilitate import in NetLogo. The user also specifies post-harvest deer density (per square mile) for the selected region using the 'PostHarvestDensity' slider. Deer distribution is known to be influenced by the amount of forest cover and availability of agricultural food (mix of forest and agricultural land) [4,5]. Individual patches are assessed for deer occupancy using parameters *min%ForestCover* and *max%ForestCover*. Patch variable *dh* is used for grouping of contiguous deer occupancy patches, thus facilitating initial distribution of deer in the model landscape. Dispersal distances for yearling male deer are also known to be influenced by percent forest cover of their natal range [6,7]. To facilitate calculation of dispersal distances during simulation, patch variable *meanForestPercent* is calculated for each non-border patch (average forest cover for a patch and its immediate neighbors). Border patches set their *meanForestPercent* equal to that of one of their non-border neighboring patch. Deer are populated on deer habitat patches at a post-harvest density and sex-age structure specific for the region. Hunting and natural mortality sliders are set for each sex- and age-class; hunting mortality is an annual rate while natural mortality rates are monthly. The user can also set the male yearling dispersal rate.

Input data

The only model input is GIS data for the sampling region along with percent forest cover for each one square mile patch in the landscape.

<u>*Submodels*</u>

1. Individual growth

This submodel is executed at the beginning of the time step. All deer in the model landscape update their state variable ‘aim’ (age in months) by one month.

2. Deer census

Post-harvest census is scheduled in the 1st month (one time step after annual harvest), and pre-harvest census in the 11th month (one time step before the annual harvest) of each year. Deer up to 1 year old are categorized as fawns, 13 months to 2 years old as yearlings and more than 25 months old as adults. Number of male and female deer in each of the three age categories is reported separately.

3. Deer group dynamics and sociality

Social structure of a host species has important implications for transmission of infectious diseases. White-tailed deer are social animals exhibiting an intermediate level of sociality, typically occurring in small, relatively stable groups of adult females and their recent offspring (doe social groups), loose bachelor groups of adult males, or as solitary individuals (male and female) [8,9]. However, the pattern and strength of social affiliations in white-tailed deer populations fluctuate temporally. For instance, pregnant females seek isolation during the fawning season and become aggressive towards other deer including group members [8,10]. Similarly, bachelor groups break up and bucks are solitary during the breeding season [1]. In this model, we include two processes, *bachelor group dynamics* and *doe group dynamics*, which facilitate simulation of group dynamics as well as within- and between-group contact patterns in the model deer populations.

Bachelor group dynamics

Adult male deer are solitary during breeding season, but otherwise form temporary bachelor groups of nonrelated individuals [1]. During the first month every year immediately after post-harvest census, potential number of bachelor groups in the deer population is calculated based on total number of adult and yearling males in the population and the parameter *mean-bachelor-group-size*.

$$Number\ of\ bachelor\ groups = \frac{yearling\ males + adult\ males}{meanbachelorgroupsize}$$

If the number of surviving bachelor group leaders from the previous year is less than the potential number of bachelor groups, the required number of randomly selected adult male deer older than 32 months is designated as potential bachelor group leaders (state variable *ml* is changed to 1). The leaders then form bachelor groups by first setting their potential group size (using the parameter *mean-bachelor-group-size*), and then recruit available adult males from patches within a 1.5 mile radius; surviving group members from the previous year are recruited before new members. Members of a bachelor group take their group leader's ID number ('who number', a built-in agent variable) as their state variable *mgroid*.

Doe group dynamics

After the fawning season (month = 5), doe social groups regulate their group size using the parameter *doe-social-group-size-regulator*. Groups with membership approaching or exceeding the value set by *doe-social-group-size-regulator* undergo fission. Up to two female group members (adults or yearling) lose their group affiliation and become solitary along with their fawns. A deer is considered a member of a doe social group when its state variable *fgroid* has the group leader's ID number, and the other state variable *gr* has a value of -1. When a doe social group member becomes solitary, *fgroid* is changed to -1 and *gr* is changed to -2. Solitary females can also be designated as leaders if the current number of group leaders in the landscape is low.

After fawning (month = 5), designated leaders of doe social groups with four or less members increase their group size by seeking solitary females in a 1.5 mile radius and adding up to two females along with their new-born fawns to the group.

Yearling dispersal

Dispersal behavior can create opportunities for the spread of pathogens like CWD [11]. Although most dispersal is done by yearling bucks [12,13], female dispersal also occurs, albeit at lower rates [14]. Dispersing individuals travel the calculated dispersal distance (described below) as an equivalent number of patches in a random direction. We assume that the number of individuals dispersing out of the model landscape is equal to the number of individuals dispersing into the model landscape. Therefore, if at any point during dispersal, if a deer moves past the edge of the model landscape (world wraps horizontally as well as vertically), it reappears on the opposite edge as a different deer (its state variable *momid* is changed to 0).

Yearling male dispersal

Yearling males lose membership of their dam's social group at the age of 13 months by changing state variable *fgroid* to 0. Yearling males disperse during two periods every year: 1) the parturition period, cued by the intersexual aggression of pregnant females; and 2) the rut period, cued by the intrasexual aggression by adult males [15]. In this model, yearling male dispersal is scheduled before parturition (month = 5) and before rutting activity (month = 11). *Yearling-male-dispersal-rate* is specified by the observer. Mean dispersal distance is predicted using the equation from [3]

$$\bar{x} = 35.07 - 48.14\, dfp$$

where *dfp* is the patch variable representing mean forest percent of the patch and its neighbors. Variance of dispersal distance is predicted using the equation from [2]

$$\log_e(s^2) = a + b\bar{x}$$

where *a* = 3.51 (SE = 0.597) and *b* = 0.77 (SE = 0.025). Dispersal distance is obtained from a log-normal distribution using the predicted mean dispersal distance and predicted variance of dispersal distance [2]. If a male yearling reaches a non-deer occupancy patch after dispersal, it is transferred to the nearest deer occupancy patch. After dispersal, the dispersing individual's state variable *mgroid* takes a value of -1.

Yearling female dispersal

Dispersal rate as well as dispersal distance in juvenile females is influenced by deer population density [14], while agnostic behavior by pregnant does just before parturition is thought to be the reason for juvenile female dispersal [16]. In this model, yearling female dispersal is scheduled before fawning (in the fifth month every year).

Proportion of yearling females that disperse is calculated using the parameter *yearling-female-dispersal-rate* and the dispersal distance for each dispersing female yearling is derived from a random distribution using parameters *mean-female-dispersal-distance* and *stddev-dispersal-distance*. If a dispersing individual reaches a non-deer occupancy patch after dispersal, it is transferred to the nearest deer occupancy patch. Dispersing yearling females change their state variables *fgroid* and *gr* to -1 and -2 respectively.

Fawning

Fawning is scheduled in the fifth month of each year, immediately after executing yearling dispersals. A proportion of female yearlings aged 13 months (determined by the parameter *juvenile-female-pregnancy-rate*), and a proportion of adult female deer (determined by the parameter *adult-female-pregnancy-rate*) are randomly selected to produce fawns (using 'hatch-deer' to create new deer). Juvenile deer give birth to one fawn and adult deer give birth to twins. Sex ratio at birth is set at 1:1 [17]. Fawns inherit two state variables from their dam: *fgroid* (female social group identifier) and *gr* (group size). Additionally, male fawns have the state variable *mgroid* set to -2.

Deer mortality

If a female group leader dies (hunting or natural mortality), leadership is either a) transferred to another adult female in the same group (new leader's state variable *gl* changes from 0 to 1; members change their state variable *fgroid* to the new leader's ID ('who number'); b) if no adult female member exists in the group, members join other small group (group size <= 3) on the same patch (change their state variable *fgroid* to the new group leader's ID); or c) the group members become solitary (change their state variables *gr* and *fgroid* to -2 and -1. If a bachelor group leader dies due to natural mortality when month ≤ 10, leadership is transferred to one of the surviving group members. If there is only one surviving group member, or when the bachelor group leader dies during the breeding season (hunting or natural mortality) when adult male deer are solitary, group leadership is not transferred.

Non-hunting mortality

The probability of a deer dying of natural or other non-hunting related causes during every time step is determined by age- and sex- specific monthly mortality rates (Table 2). Irrespective of these rates, old deer (>240 months) have an overall high probability of dying (0.8) during a time step. Fawns are functional ruminants at two months of age [18], and therefore can possibly survive the death of their mother. We assume that fawns less than two months old do not survive if their mother dies. If members of a doe social group die during a time step, the group leader's state variable *gr* (accounting for the group size) is decreased accordingly. If there are no members remaining in a group, the leader becomes a solitary deer (state variables *fgroid* and *gr* changed to -1 and -2 respectively).

Hunting mortality

Hunting mortality is scheduled one time step after the rut period. Deer surviving the monthly non-hunting mortality execute the hunting mortality submodel. The probability of a deer being included in the hunter harvest is specified by the age- and sex- specific hunting mortality rates (Table 2).

Parameterization and Calibration

MO*Ov*POP has a total of 33 parameters; the user can select values for 17 parameters from a range of values using sliders on the model interface before executing the model. Parameter values are obtained from peer-reviewed literature, derived from field-based surveys, or are based on expert opinions.

Population dynamics of the model deer population is defined by two sets of age-sex-specific parameters, *hunting mortality rates* and *non-hunting mortality rates*. We classify deer in four age-classes: young fawns (up to 6 months old), older fawns (7 to 12 months old), yearlings (13 to 24 months old) and adults (25 months or older). It should be noted that non-hunting mortality rates are per month rates (Table 2).

The model interface has sliders to set values of age-sex-specific hunting and non-hunting mortality rates.

During initial setup, four parameters define the abundance and structure of deer population: *PostHarvestDensity*, *sexratio*, *adultprop* and *yearlingprop* (Table 3). Post-harvest deer density is specified by the user. The proportion of fawns in the initial population is calculated by subtracting the sum of *adultprop* and *yearlingprop* from 1 (proportion of fawns = 1 – [*adultprop* + *yearlingprop*]). Further, deer occupancy on patches in the model landscape is defined by two parameters, *min%ForestCover* and *max%ForestCover*. Deer thrive in landscapes with at least 25% forest [19], and do well in landscapes where forest cover and agricultural food are juxtaposed and readily available [4,20]. We have therefore set the values for *min%ForestCover* and *max%ForestCover* at 25% and 75% respectively.

Bachelor group size is regulated by the parameter *mean-bachelor-group-size*, while doe social group size is regulated by the parameter *doe-group-size-regulator*. Doe social group size ranges between 2 and 12 [21,22], but smaller group sizes (less than 8) are commonly seen in Missouri (L. Hansen, personal communication). Bachelor group size ranges between 2 and 5 [18,23,24]. We calibrated parameter values for *mean-bachelor-group-size* and *doe-group-size-regulator* so that the model group sizes are in agreement with the references and expert opinions (Table 3).

Body mass attained during the breeding season appears to be a strong determinant of a fawn’s ability to breed [25]. The percent of female fawns that breed is influenced by the population’s level of nutrition. We have set the value of *breeding-prop-female-fawns* at 20%, based on data from an ongoing deer study in Missouri (Jon McRoberts, personal communication).

Dispersal rates for yearling males range between 46 and 80% [3], but no predictive relationships are yet known [2]. We have assumed a 46% rate for yearling male dispersal in the simulations described in this paper. Dispersal rate for juvenile females in west-central Illinois was 22% and in Pennsylvania it was 12% [26,27]. A study undertaken in Pennsylvania documented an average dispersal distance of 18.0 ±7.0 km [27]. For deer densities prevalent in Missouri, the logistic regression model based on meta-analysis of dispersal data from peer-reviewed literature predicted similar dispersal rates and distances for juvenile female deer [14]. For the simulations described in this paper, parameter *yearling-female-dispersal-rate* is set at 22%, *mean-female-dispersal-distance* is set at 11 miles and *stddev-dispersal-distance* is set at 4 miles.

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Table1. Agents included in MO*Ov*POP*surveillance* and their state variables. All state variables except the deer state variable ‘*aim*’ are unitless.

Agent	Variable	Description
Patch	forest-percent	forest cover on a patch expressed as a proportion
	border	patches at the edge of the model landscape have border = 1, other patches have border = 0
	dfp	mean forest-percent calculated for a patch and its immediate neighbors
	dh	deer habitat; ≥ 1 if a patch qualifies as deer habitat, < 1 if it is not a deer habitat
	do	deer occupancy; 1 if deer occur on a patch, 0 if not
	add	average deer density for a patch and its eight neighbors
Deer	sex	1 if male, 2 if female
	aim	age in months
	momid	mother’s id number
	gl	1 if doe social group leader, 0 otherwise
	ml	1 if bachelor group leader, 0 otherwise
	fgroid	≥ 0 if member of a doe social group, -1 if solitary female, 0 for male deer
	gr	for doe social group leaders, gr denotes the number of group members; -1 for non-leader members of a doe social group, -2 if for solitary female deer, and 0 for all yearling and adult male deer
	mgroid	0 for all females, -2 for male fawns, -1 for male yearlings , and for bachelor group members it takes the value of group leader id

Table 2. Age- and sex-specific mortality parameter values used in MO*Ov*POP and MO*Ov*POP*surveillance*.

Parameter	Description	Value
Non-hunting mortality		
mf6nhm	male fawns (0 - 6 months)	0.055 per month [a]
ff6nhm	female fawns (0 - 6 months)	0.055 per month [a]
mf12nhm	male fawns (7 - 12 months)	0.05 per month [b]
ff12nhm	female fawns (7 - 12 months)	0.05 per month [b]
mynhm	male yearlings (13 - 24 months)	0.01 per month [b]
fynhm	female yearlings (13 - 24 months)	0.00 per month [b]
manhm	male adults (> 25 months)	0.01 per month [b]
fanhm	female adults (> 25 months)	0.02 per month [b]
Hunting mortality		
mf6hm	male fawns (0 - 6 months)	0 [c]
ff6hm	female fawns (0 - 6 months)	0 [c]
mf12hm	male fawns (7 - 12 months)	0.05 per year [c]
ff12hm	female fawns (7 - 12 months)	0.02 per year [c]
myhm	male yearlings (13 - 24 months)	0.25 per year [c]
fyhm	male yearlings (13 - 24 months)	0.15 per year [c]
mahm	male adults (> 25 months)	0.40 per year [c]
fahm	male adults (> 25 months)	0.20 per year [c]

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[c] Derived from hunter-harvest data collected by Missouri Department of Conservation.

Table 3. Parameter values used in MOOvPOP for initial population and behavior (group formation, dispersal, pre-breeding and breeding interactions) of white-tailed deer in Franklin County, MO. An asterix indicates calibrated values.

Parameter	Description	Value
Initial population setup and distribution		
PostHarvestDensity	Density of deer after the harvest season	20 per square mile [a]
sexratio	Male : female ratio in the population	1:1.2 [a]
adultprop	Proportion of adults (≥ 25 months) in the population	0.4 [a]
yearlingprop	Proportion of yearlings in the population	0.25 [a]
min%ForestCover	Minimum percent forest cover of deer habitat patch	0.25 [42]
max%ForestCover	Maximum percent forest cover of deer habitat patch	0.75 *[23,43]
Behavior		
mean-bachelor-group-size	mean (± standard deviation) number of adult male deer in a bachelor group	4 ± 1 *[41,46,47]
doe-group-size-regulator	group size (after fawning season) above which a doe social group undergoes fission	6 *[44,45] b
breeding-prop-female-fawns	proportion of fawns that reproduce	0.2 [c]
yearling-male-dispersal-rate	proportion of yearling male deer that disperse from their natal range	0.46 [21,22]
yearling-female-dispersal-rate	proportion of yearling females that disperse from their natal range	0.22 *[19]
mean-female-dispersal-distance	mean dispersal distance for yearling female deer	11 miles *[19]
stddev-dispersal-distance	standard deviation for the mean dispersal distance of yearling female deer	4 miles *[19]

[a] Derived from hunter-harvest data collected by Missouri Department of Conservation.

[b] L. Hansen, pers.comm

[c] J. McRoberts, pers. comm