Documentation for IN*Ov*POP

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IN*Ov*POP (INdiana *Odocoileus virginianus* POPulation dynamics)

Purpose

IN*Ov*POP is designed to simulate white-tailed deer (*Odocoileus virginianus*) population dynamics (abundance, sex-age composition and distribution in the landscape) in user-specified landscapes (Indiana counties), and generate realistic pre- and post-harvest population snapshots. The deer population snapshots can be used to initialize IN*Ov*CWD (an ABM that simulates the spread of chronic wasting disease (CWD) in deer). The importance of individual heterogeneity in the study of host-pathogen systems is increasingly being recognized. ABMs can incorporate stochastic and heterogeneous processes, and are therefore particularly useful for elucidating the interplay between individual host heterogeneities, demographic and environmental stochasticities and wildlife disease dynamics.

CWD is an emerging prion disease of North American cervids (white-tailed deer, mule deer *Odocoileus hemionus*, and elk *Cervus elaphus*), and represents a unique challenge for wildlife agencies in the United States. IN*Ov*POP and IN*Ov*CWD together provide a decision-making framework for designing CWD surveillance and management strategies. This model builds upon the ABM developed for simulating Missouri's white-tailed deer populations, MO*Ov*POP (https://www.comses.net/codebases/5585/releases/2.1.2/) described by Belsare et al. [1].

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<u>*Entities, state variables and scales*</u>

Spatial scales: IN*Ov*POP has a spatially-explicit landscape that can be set up for individual counties or CWD management zones using GIS coverage data (forest cover) for the selected region. Irrespective of the region selected for simulation, each patch in the model landscape represents one square mile. 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: IN*Ov*POP has a monthly time step, and duration of the simulation is 25 years. The main reason we project the deer population over a 25 year period is to ensure that the population snapshot is obtained after age-sex class composition stabilizes and lambda (population growth rate) equilibrates at around 1.

Entities: IN*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 that occur on patches in the model landscape.

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).

Table1. Agents included in IN*Ov*POP 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
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
	groid	≥ 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 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

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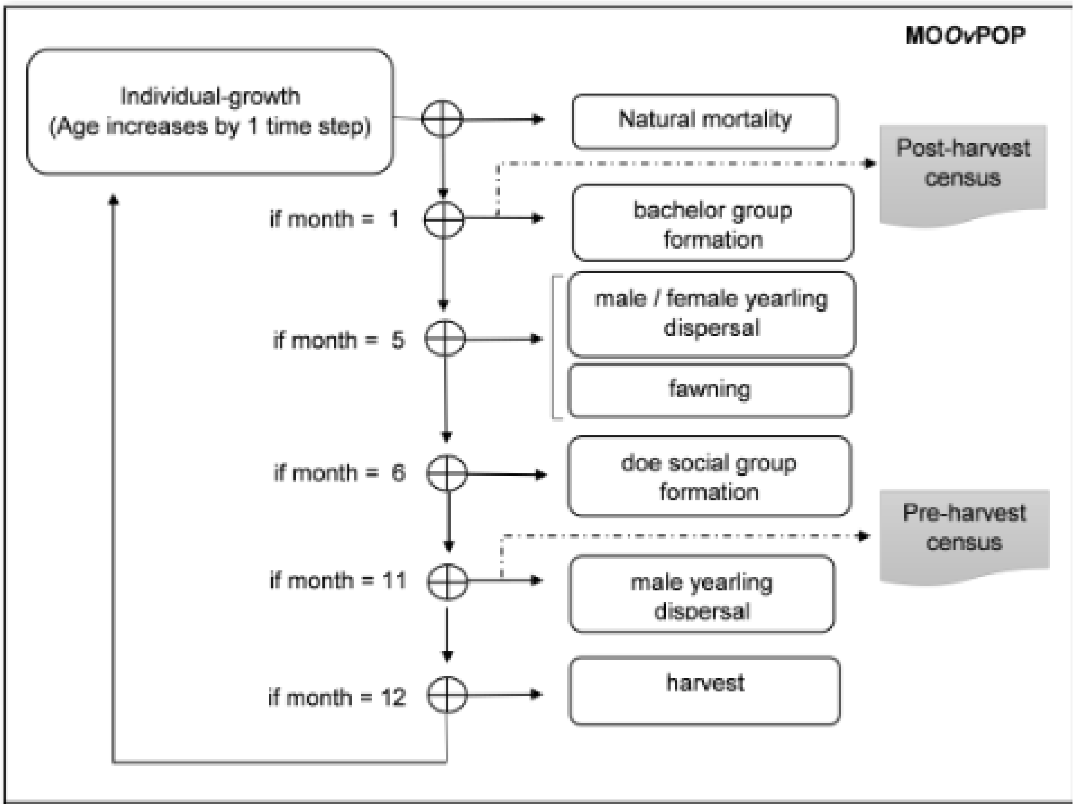
Process overview and scheduling

Processes: Processes included in this model are all related to deer: individual growth (aging), male and female yearling dispersal, bachelor group formation, doe social group formation, fawning, hunting and non-hunting mortality (Figure 1). 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 [2]. To model group dynamics, one adult member of each doe social group and bachelor group was designated as leader.

Schedule: Individual growth (increase in age by one month) is scheduled at the beginning of each time step and is followed by non-hunting mortality. This is followed by time step specific processes: bachelor group formation (month = 1), male and female yearling dispersal followed by fawning (month = 5), male yearling dispersal (month = 11) and harvest (month = 12). Group size is updated after any group member executes birth, death or dispersal process. Census and plotting graphs (observer actions) are scheduled at the end of each time step. The month counter resets after every 12 months.

Fig 1. Schedule of processes in IN*Ov*POP.



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.

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

Adaptation: Fawns (both male and female) entering the yearling class make a decision whether to disperse and leave their natal group. Members of doe social groups update and regulate their group size in response to mortality or birth events involving group members. Group leadership is transferred if a group leader dies.

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

Stochasticity: Each individual deer in the model is subject to a mortality probability during a time step. The mortality probability is derived from the mortality rate (natural or hunting). Male and female group leaders are selected from a set of potential candidates during the setup, or when leaders have to be replaced due to mortality events.

Observation: IN*Ov*POP has a graphical display of deer distribution in the landscape. Deer abundance and distribution are updated as the model executes. Additionally, three graphical displays are included: one plots deer abundance versus time, and the other two plot frequency distribution of bachelor and doe social group sizes respectively. Monitors display number of deer in each age-sex-class. Pre-harvest and post-harvest population abundance by age-sex class is recorded in an output file for each year of model run.

Initialization

IN*Ov*POP is initialized with forest cover data and post-harvest deer density for the desired sampling region. Forest cover data (United States Geological Survey 1992 National Land Cover Data) for selected sampling regions in Michigan was converted to a forest percentage grid of 1 square mile patches to facilitate import in NetLogo. Model deer population for a sampling region is initialized using post-harvest density (deer per square mile), age composition (fawns: yearlings: adults), M: F ratio and age-sex mortality parameters derived from regional deer harvest data and expert opinions.

Input data

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

Submodels

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. Number of male and female deer in each age-class 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) [3,4]. 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 [3,5]. Similarly, bachelor groups break up and bucks are solitary during the breeding season [2].

Bachelor group dynamics

Adult male deer are solitary during breeding season, but otherwise form temporary bachelor groups of nonrelated individuals [2]. 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*.

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

Surviving bachelor group leaders from the previous year maintain their leader status. If the potential number of bachelor groups exceed the available number of group leaders, an appropriate number of bucks older than 32 months are randomly selected and designated as potential bachelor group leaders. The leaders then form bachelor groups by first setting their potential group size (using the parameter *mean-bachelor-group-size*), and then recruiting available adult bucks from patches within a 1.5 mile radius; surviving group members from the previous year are recruited before new members.

Yearling dispersal

The proportion of dispersing yearlings is set using two parameters: *yearling-male-dispersal-rate* and *yearling-female-dispersal-rate*. 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, 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

Dispersal distances for yearling bucks are modeled using percent forest cover, as suggested by Diefenbach et al. [6]. Average forest cover for a patch and its immediate neighbors is first calculated for each non-border patch and the value is stored as a patch variable (*dfp*). Border patches set their *dfp* equal to that of one of their non-border neighboring patches. Mean dispersal distance is predicted using the equation from [7]

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

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 [6]

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

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 [6]. 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. Group size of the dispersing deer’s natal group is updated.

Yearling female dispersal

Dispersal distance for dispersing juvenile female 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 *groid* and *gr* to -1 and -2 respectively. Group size of the dispersing deer’s natal group is updated.

Fawning

A proportion of female yearlings aged 13 months (determined by the parameter *juvenile-pregnancy-rate*), and a proportion of adult female deer (determined by the parameter *adult-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 (MDC data). Sex ratio at birth is set at 1:1 [8]. Fawns inherit two state variables from their dam: *groid* (female social group identifier) and *gr* (group size). Additionally, male fawns have the state variable *mgroid* set to -2.

After the fawning season (month = 5), doe social groups update, and if necessary, regulate their group size. If the group size is greater than 6 (value set by the reporter *doe-social-group-size-regulator*; see Parameterization and Calibration), up to two female group members (adults or yearling) along with their fawns lose group affiliation and become solitary. A deer is considered a member of a doe social group when its state variable *groid* has the group leader's ID number, and the other state variable *gr* has a value of -1. 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.

Deer mortality

If a female group leader dies (hunting or natural mortality), leadership is 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 *groid* to the new leader's ID ('who number'); b) if no adult female member exists in the group, surviving members join another group on the same patch with group size <= 3 (change their state variable *groid* to the new group leader's ID); c) if no small group is available on their patch, the surviving group members become solitary (change their state variables *gr* and *groid* to -2 and -1, respectively).

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).

If a bachelor group leader dies due to natural mortality, leadership is transferred to one of the surviving group members. If there are no members remaining in a bachelor group, the leader changes its status to solitary (state variable ml changed to 0).

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 [9,10]. 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 [11], 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.

Hunting mortality

Hunting is the leading cause of deer mortality in most areas of the Midwest [12]. The largest portion of the annual harvest happens during the firearms portion of the deer harvest (usually scheduled between mid- to late November until the 1st week of January), and accounts for most of the samples collected for CWD testing. In this model, harvest is simulated to occur in the 12th time-step every year, one time step after the rut period. Number of deer harvested is specified by age- and sex- specific hunting mortality rates derived from hunter-harvest data collected (Table 2). In MI*Ov*POP, deer surviving the monthly non-hunting mortality are randomly selected to execute the hunting mortality submodel.

Table 2. Age- and sex-specific mortality parameter values used in MI*Ov*POP. These values are derived from harvest data collected by the Michigan Department of Natural Resources or expert opinions.

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)	0.07 per year [c]
ff12hm	female fawns (7 - 12 months)	0.09 per year [c]
myhm	male yearlings (13 - 24 months)	0.42 per year [c]
fyhm	male yearlings (13 - 24 months)	0.22 per year [c]
mahm	male adults (> 25 months)	0.35 per year [c]
fahm	male adults (> 25 months)	0.118 per year [c]

[a] Hiller, T.L., Campa III, H., Winterstein, S.R., Rudolph, B.A., 2008. Survival and space use of fawn white-tailed deer in southern Michigan. The American Midland Naturalist 159, 403-412.

[b] Van Deelen, T.R., Campa III, H., Haufler, J.B., Thompson, P.D., 1997. Mortality patterns of white-tailed deer in Michigan's Upper Peninsula. The Journal of wildlife management, 903-910.

[c] Derived from hunter-harvest data from a representative Midwest region (Michigan- Michigan DNR).

Parameterization and Calibration

User-specified information (landscape, vital rates, harvest rates) underpins model the dynamics in this model. Population parameters used to initialize the model deer population, simulate deer behavior or validate model outputs are derived from peer-reviewed literature, field-based surveys, harvest data, or are based on expert opinions (Tables 2 and 3). During initial setup, the abundance and the structure of deer population is determined by four user-specified population parameters: *post_harvest_density*, *sexratio*, *adultprop* and *yearlingprop*. 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*]). 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*. Hunting mortality rates are annual, while non-hunting mortality rates are monthly rates. The model interface has sliders to set values of age-sex-specific hunting and non-hunting mortality rates.

Further, deer occupancy on patches in the model landscape is defined by two parameters, *min-forestcover-percent* and *max-forestcover-percent*. Deer thrive in landscapes with at least 25% forest [12], and do well in landscapes where forest cover and agricultural food are juxtaposed and readily available [13,14]. We have therefore set the values for *min-forestcover-percent* and *max-forestcover-percent* at 25% and 75% respectively.

Group sizes in the model are regulated using reporters, *mean-bachelor-group-size* and *doe-group-size-regulator*. Values for *mean-bachelor-group-size* and *doe-group-size-regulator* were calibrated so that the model group sizes remained within the range derived from the literature and expert opinion (Table 3).Doe social group size ranges between 2 and 12 [15,16], but smaller group sizes (less than 8) are commonly seen in the Midwestern US, and bachelor group size typically ranges between 2 and 5 [11,17,18], but larger groups of up to 8 are occasionally seen in this region (L. Hansen, personal observation).

Body mass attained during the breeding season appears to be a strong determinant of a fawn's ability to breed [19]. 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 bucks range between 46 and 80% [7] but predictive relationships are poorly understood [6]. We have set the yearling buck dispersal rate at 46% for simulations described in this paper. Similarly, based on observations from west-central Illinois, the juvenile female dispersal rate is set at 22% [20]. Mean dispersal distance for juvenile females was set at 11 miles – this value was extrapolated for a post-harvest deer density of ~25 per forested km^2 from a logistic regression model based on meta-analysis of juvenile female dispersal data [21].

Values for parameters *min-forestcover-percent*, *max-forestcover-percent, mean-bachelor-group-size, doe-group-size-regulator, breeding-prop-female-fawns, yearling-female-dispersal-rate, mean-female-dispersal-distance, stddev-dispersal-distance* are accessed during the code execution using 'to-report'.

Table 3. Parameter values derived from peer-reviewed literature, field-based surveys or expert opinions for use in IN*Ov*POP. 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 Michigan DNR's data.

[b] L. Hansen, pers.obs

[c] J. McRoberts, pers. comm

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