# Documentation for MO*Ov*POP

## *Purpose*

MO*Ov*POP is designed to simulate population dynamics (abundance, sex-age composition and distribution in the landscape) of white-tailed deer (*Odocoileus virginianus*) for a selected sampling region. These population data can be used to initialize MO*Ov*POP*surveillance*, another agent-based model, that can be used to guide collection and analysis of disease surveillance data that relies on non-probabilistic methods like harvest-based sampling.

Harvest-based sampling plays an important in the surveillance of many important wildlife diseases. Chronic wasting disease (CWD) is one such 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. An ABM approach can incorporate a large degree of heterogeneity and therefore is especially useful in the study of wildlife diseases like chronic wasting disease (CWD).

## *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).

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

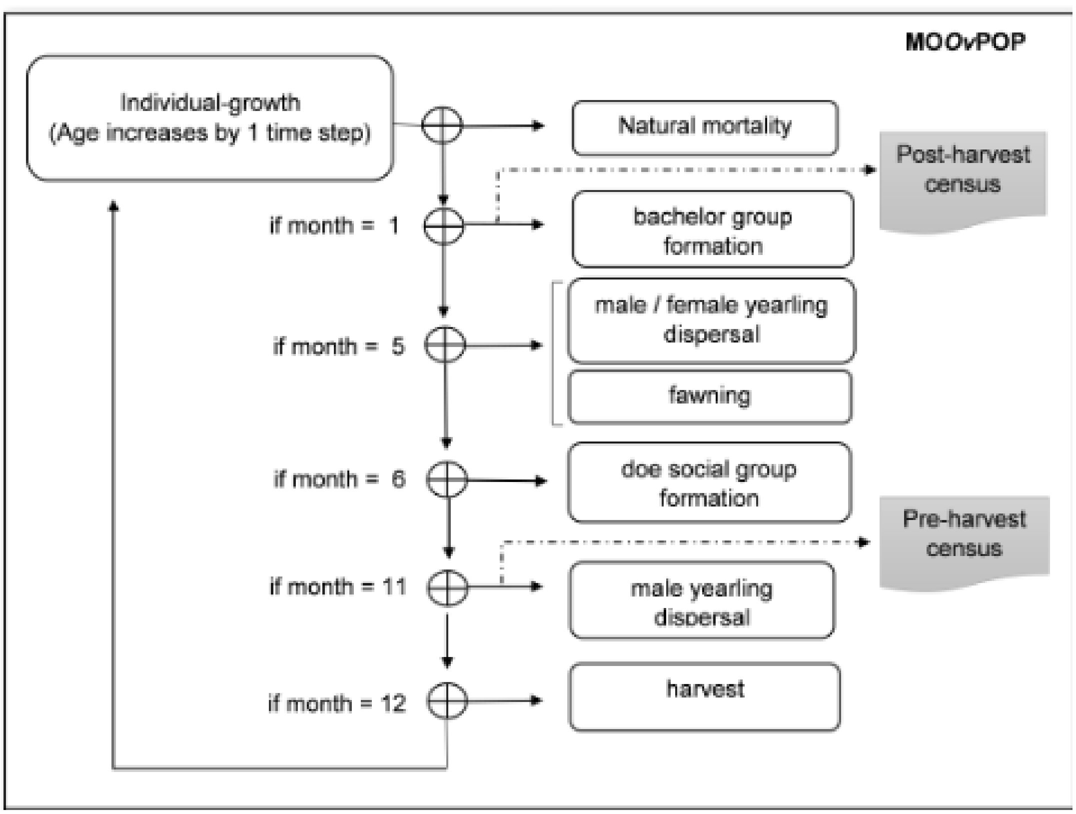
| Agent | Variable | Description |
|---|---|---|
| **Patch** | forest-percent | forest cover on a patch expressed as a proportion |
| | border | patches at the edge of the model landscape have border = 1, other patches have border = 0 |
| | dfp | mean forest-percent calculated for a patch and its immediate 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 |
| **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 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 |

*<u>Process overview and scheduling</u>*

*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 (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 [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.

**Fig 1. Schedule of processes in MO*Ov*POP and MO*Ov*POP*surveillance*.**



*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 (*PreHarvestPopulation*). 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 *post_harvest_density* 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-percent* and *max-forestcover-percent*. 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, the average forest cover for a patch (patch and its immediate neighbors) is calculated for each non-border patch. In case of border patches, average forest cover is set to that of one of their non-border neighboring patches. 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.

*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 1$^{st}$ month (one time step after annual harvest), and pre-harvest census in the 11$^{th}$ 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).

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] |

[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 collected by Missouri Department of Conservation.

*<u>Parameterization and Calibration</u>*

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: *post_harvest_density*, *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-percent* and *max-forestcover-percent*. 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-percent* and *max-forestcover-percent* 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 observation). 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.

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 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.obs
[c] J. McRoberts, pers. comm

*How to use the model:*

1. Download the model: https://www.openabm.org/model/5585/version/6/view Model Files -> Code -> click on MO*Ov*POP_v2.nlogo. The model should open in NetLogo 6. Ensure that the latest version is selected. Save this model in a folder on your computer.
2. Download GIS files (zip folder *gis_files_MOOvPOP*) in the same folder, and extract all the files. These files should be in the same folder as the NetLogo model file (MO*Ov*POP).
3. Open MO*Ov*POP.
4. Choose an option for the Chooser 'Output2'. File/s (.csv) for the desired output will be created in the folder where the model is saved (prehpopCountyName.csv and/or posthpopCountyName.csv).
5. Click on the Interface tab. Select Region (Click on the red triangle to see a drop down menu).
6. Use sliders provided on the interface to specify a) *post_harvest_density*: deer per square mile in the selected region b) *sexratio*: females per 100 deer in the post-harvest population c) *adultprop*: proportion of adult deer in the post-harvest population d) *yearlingprop*: proportion of yearling deer in the post-harvest population e) non-hunting and hunting mortality rates (NOTE: Calibrated parameter values for each county can also be selected by setting the chooser to 'On' position.)
7. Click 'Setup'. Once the 'Setup' is completed, click 'Go'.

**References**


1. Hirth D. Social behavor of white-tailed deer in relation to habitat. Wildl Monogr. 1977;53: 1–55.
2. Diefenbach DR, Long ES, Rosenberry CS, Wallingford BD, Smith DR. Modeling distribution of dispersal distances in male white-tailed deer. J Wildl Manage. 2008;72: 1296–1303. doi:10.2193/2007-436
3. Long ES, Diefenbach DR, Rosenberry CS, Wallingford BD, Grund MD. Forest cover influences dispersal distance of white-tailed deer. J Mammal. 2005;86: 623–629. doi:http://dx.doi.org/10.1644/1545-1542(2005)86[623:FCIDDO]2.0.CO;2
4. VerCauteren KC, Hygnstrom SE. White-tailed deer. In: Wishart D, editor. Encyclopedia of the Great Plains. Lincoln, NE: University of Nebraska Press; 2004. pp. 642–643.
5. Walter WD, VerCauteren KC, Campa HIII, Clark WR, Fischer JW, Hygnstrom SE, et al. Regional assessment on influence of landscape configuration and connectivity on range size of white-tailed deer. Landsc Ecol. 2009;24: 1405–1420.
6. Muñoz PM, Boadella M, Arnal M, de Miguel MJ, Revilla M, Martínez D, et al. Spatial distribution and risk factors of brucellosis in Iberian wild ungulates. BMC Infect Dis. 2010;10: 46. doi:10.1186/1471-2334-10-46
7. Dusek RJ, Bortner JB, DeLiberto TJ, Hoskins J, Franson JC, Bales BD, et al. Surveillance for high pathogenicity avian influenza virus in wild birds in the Pacific Flyway of the United States, 2006-2007. Avian Dis. 2009;53: 222–230. doi:10.1637/8854.1
8. Ozoga J., Verme L., Bienz C. Parturition behavior and territoriality in white-tailed deer: Impacts on neonatal mortality. J Wildl Manage. 1982;46: 1–11.
9. Monteith KL, Sexton CL, Jenks JA, Terry Bowyer R. Evaluation of techniques for categorizing group membership of white-tailed deer. J Wildl Manage. 2007;71: 1712–1716.

10. Schwede G, Hendrichs H, McShea W. Social and spatial organization of female white-tailed deer, Odocoileus virginianus, during the fawning period. Anim Behav. 1993;45: 1007–1017.

11. Cullingham CI, Merrill EH, Pybus MJ, Bollinger TK, Wilson GA, Coltman DW. Broad and fine-scale genetic analysis of white-tailed deer populations: Estimating the relative risk of chronic wasting disease spread. Evol Appl. 2011;4: 116–131. doi:10.1111/j.1752-4571.2010.00142.x

12. Nelson ME. Natal dispersal and gene flow in white-tailed deer in northeastern Minnesota. J Mammal. 1993;74: 316–322.

13. Purdue JR, Smith MH, Patton JC. Female philopatry and extreme spatial genetic heterogeneity in white-tailed deer. J Mammal. 2000;81: 179–185.

14. Lutz CL, Diefenbach DR, Rosenberry CS. Population density influences dispersal in female white-tailed deer. J Mammal. 2015;96: 494–501.

15. Long ES, Diefenbach DR, Rosenberry CS, Wallingford BD. Multiple proximate and ultimate causes of natal dispersal in white-tailed deer. Behav Ecol. 2008;19: 1235–1242.

16. Lutz CL, Diefenbach DR, Rosenberry CS. Proximate influences on female dispersal in white-tailed deer. J Wildl Manage. 2016;80: 1218–1226.

17. Ditchkoff SS. Anatomy and Physiology. In: Hewitt DG, editor. Biology and management of white-tailed deer. Boca Raton, FL: CRC Press; 2011. pp. 43–73.

18. Marchinton RL, Hirth D. Behavior. In: Halls LK, editor. White-tailed deer: Ecology and management. Harrisburg, PA: Stackpole Books; 1984. pp. 129–168.

19. VerCauteren KC, Hygnstrom SE. Managing White-tailed Deer: Midwest North America. In: Hewitt DG, editor. Biology and management of white-tailed deer. 1st ed. Boca Raton, FL: CRC Press; 2011. pp. 501–535.

20. Walter WD, VerCauteren KC, Campa H, Clark WR, Fischer JW, Hygnstrom SE, et al. Regional assessment on influence of landscape configuration and connectivity

on range size of white-tailed deer. Landsc Ecol. 2010;24: 1405–1420. doi:10.1007/s10980-009-9374-4

21. Nelson ME, Mech LD. Dispersal in female white-tailed deer. J Mammal. 1992;73: 891–894.

22. Miller BF, DeYoung R., Campbell TA, Laseter BR, Ford WM, Miller KV. Fine-scale genetic and social structuring in a central Appalachian white-tailed deer herd. J Mammal. 2010;93: 681–689.

23. Smith, W P. Odocoileus virginianus. Mamm Species. 1991;388: 1–13.

24. Miller KV, Muller LI, Demarias S. White-tailed deer (Odocoileus virginianus). In: Feldhamer GA, Thompson BC, Chapman JA, editors. Wild mammals of North America: Biology, management, and conservation. 2nd ed. Baltimore, Maryland: Johns Hopkins University Press; 2003. pp. 906–930.

25. Gaillard JM, Festa-Blanchet M, Yoccoz N., Loison A, Toigo C. Temporal variation in fitness components and population dynamics of large herbivores. Annu Rev Ecol Syst. 2000;31: 367–393.

26. Nixon CM, Mankin PC, Etter DR, Hansen LP, Brewer PA, Chelsvig JE, et al. White-tailed deer dispersal behavior in an agricultural environment. Am Midl Nat. 2007;157: 212–220.

27. Lutz CL, Diefenbach DR, Rosenberry CS. Proximate influences on female dispersal in white-tailed deer. J Wildl Manage. 2016;80: 1218–1226.