ODD for IN*Ov*CWD

IN*Ov*CWD (Indiana *Odocoileus virginianus* Chronic Wasting Disease dynamics)

Background

Chronic wasting disease (CWD) is an emerging prion disease of North American cervids (including white-tailed deer *Odocoileus virginianus*, mule deer *Odocoileus hemionus*, and elk *Cervus canadensis*) that is being actively managed by wildlife agencies in many states and provinces in North America.

Disease transmission models are valuable tools for investigating wildlife disease dynamics and informing disease management strategies (Pepin et al., 2014). For any directly transmitted infectious disease, transmission is influenced by host behavior, movement patterns, and social structures including emergent contact networks (Altizer et al., 2003; Cross et al., 2009). Agent-based models (ABMs) can incorporate host population structure, social organization and host behavior, and different sources of host mortality (e.g., disease- or harvest-mediated removals). Therefore, ABMs are particularly useful to understand disease spread dynamics and the impact of CWD control efforts, measured by metrics such as, rate of disease spread and outbreak probability.

Purpose

IN*Ov*CWD simulates CWD spread in an *in silico*, realistic white-tailed deer population in Indiana. Management interventions can be evaluated by iterating IN*Ov*CWD using different scenarios (e.g. alternate harvest management strategies).

Entities, state variables and scales

Entities: IN*Ov*CWD has two entities: patches and deer. Deer are modeled as individuals that occur on patches that have suitable habitat conditions relevant to white-tailed deer.

State variables: Patch state variables are inherited from the population dynamics model (IN*Ov*POP). Each patch is characterized by its percent forest cover (*forest-percent*), whether it is located on one of the edges of the model landscape (*border*), whether it qualifies as a deer habitat (*dh*), whether deer occur on the patch (*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 (Moore neighborhood, a cell and its 8 adjacent neighbors). Each deer has fifteen state variables, which define individual characteristics like age, sex, group membership and status, mating behavior, CWD infection status, and the duration of CWD phases (pre-infectious, pre-clinical, total course of disease) (Table 1).

Spatial scales: IN*Ov*CWD can be configured for any individual county in Indiana. Each patch in the model landscape represents one square mile. Miles (rather than kilometers) were selected as the distance and area measure 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 local agencies.

Temporal scale: IN*Ov*CWD runs on a monthly time step and allows the user to define an overall simulation period in years that is dependent on application needs. For most applications, we have selected a 10-year period.

Process overview and scheduling

Processes: Processes are informed by deer and disease ecology: individual growth (aging), male and female yearling dispersal, bachelor group formation, doe social group formation, mating, fawning, hunting and non-hunting mortality, CWD progression (and transmission) (Figure 1). Transmission is an individual level process that is influenced by host contact structure and behavior. Contact pattern and interactions between deer in a population is influenced by group affiliation (Schauber, Nielsen, Kjær, Anderson, & Storm, 2015). 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 (Hirth, 1977). To model group dynamics, one adult member of each doe social group and bachelor group is designated as leader. In this model, group affiliation, and therefore the contact network, is simulated as a dynamic process that changes seasonally as well as in response to demographic processes (e.g. births, deaths).

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 and CWD progression in infected individuals. Infectious individuals transmit disease to susceptible individuals in contact. This is followed by time-step specific processes that match the ecology and timing of known deer behaviors: bachelor group formation (month = 1), male and female yearling dispersal followed by fawning (month = 5), male yearling dispersal followed by mating (month = 11), and harvest (month = 12). Group size is updated after any group member executes birth, death or dispersal process. Plotting of graphs (observer actions) is scheduled at the end of each time step. The month counter resets after every 12 months.

Table1. Agents included in IN*Ov*CWD and their state variables.

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 (Moore neighborhood)
	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 females, -2 for male fawns, -1 for male yearlings, and group leader if for bachelor group members
	nm	maximum number of matings per doe during rut period
	anm	counter for actual number of matings during a rut season
	cwd	CWD infection status (0 if uninfected, 1 if infected)
	cwdm	course of infection – from exposure to death. 22 – 26 months.
	cwdi	duration of pre-infectious phase - from exposure to the onset of infectious phase. 6 – 10 months.
	cwdc	duration of pre-clinical phase - time from exposure to the onset of clinical signs. 21 – 25 months.
	cwdpr	CWD progression (counter for months since exposure)

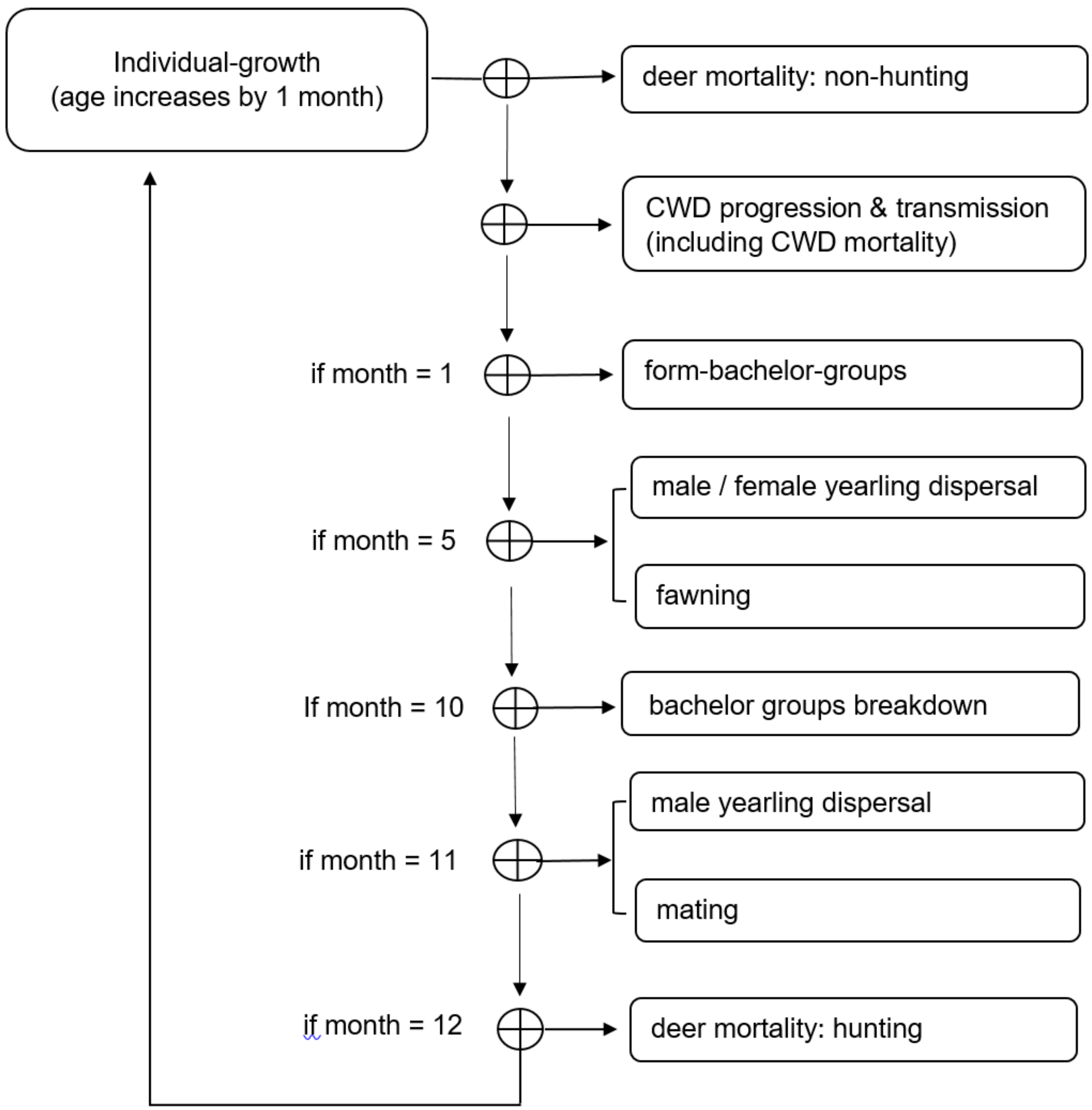

Fig 1. Schedule of processes in IN*Ov*CWD.

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. These processes have been incorporated in the model to reflect the heterogeneity observed in real-world host populations.

Emergence: Age and sex structure of the model deer population as well as the pattern of CWD spread (prevalence, age-sex wise distribution of infected deer) emerge from model processes.

Adaptation: Fawns (both male and female) entering the yearling class either disperse, or remain, in their natal group. Doe social group members 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 (Moore neighborhood - a patch and eight adjacent patches, nine square mile area).

Interaction: Group dynamics and sociality are included in IN*Ov*CWD to implicitly simulate within- and between- group interactions in the deer population. To model direct transmission of CWD, interactions between infectious and susceptible deer are explicitly incorporated. The contact probabilities are informed by a user-customizable contact matrix (*contactstructure.csv*) based on published and expert informed information. The contact matrix informs all direct transmission events in the simulated environment. Additionally, mating interactions are also included in this model.

Stochasticity: Mortality is a stochastic event in IN*Ov*CWD as individual deer are subject to mortality probabilities (natural and hunting) during each time step. Mortality probabilities are derived from user-specified mortality rates. Similarly, duration of disease phases in individual deer (pre-infectious phase, pre-clinical or latent phase, and total course of CWD) incorporate stochasticity.

Collectives: Individual deer can be affiliated with groups or can be solitary. 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 (Hirth, 1977). To model group dynamics, one adult member of each doe social group and bachelor group is designated as the leader.

Observation: For each year of the model run, pre-harvest abundance, age-sex specific harvest, number of harvested deer that were tested for CWD, number of CWD+ deer in the population before harvest, number of patches that have CWD+ deer, number of CWD+ deer in the harvest and the number of CWD+ deer in the test samples are recorded. These outputs can be used to estimate CWD outbreak probability and the rate of CWD spread (change in prevalence as well as geographic spread).

Initialization

IN*Ov*POP-generated deer population snapshot for the region of interest is used to initialize IN*Ov*CWD. MI*Ov*POP generates a realistic population snapshot for the region of interest because model population parameters like age composition (fawns: yearlings: adults), M: F ratio and age-sex mortality are derived from regional deer harvest data (collected by DNR) and/ or expert opinions.

A separate user-specified contact matrix (contactstructure.csv) determines contact probabilities for infectious contacts during each time step.

Input data

User-specified contact matrix (*contactstructure.csv*) facilitates calculation of contact probabilities between an infected and susceptible deer during a time step.

<u>*Submodels*</u>

1. *Individual growth*

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

2. *Deer mortality*

Deer mortality occurs by hunting, disease, and natural mortality sources according to sex- and age- specific probabilities. Individual mortality triggers a series of decision points for agents. 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 adjusted 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).

a) 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 (Van Deelen, Campa Iii, Haufler, & Thompson, 1997; Hiller, Henry Campa, & Winterstein, 2008). 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 (Marchinton & Hirth, 1984), 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.

b) Hunting mortality

Hunting is the leading cause of deer mortality in most areas of the Midwest (VerCauteren & Hygnstrom, 2011). 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. Harvest is simulated to occur in the 12^{th} 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). Deer surviving the monthly non-hunting mortality are randomly selected to execute the hunting mortality submodel.

c) CWD mortality

We have incorporated stochastic variation in the total duration of CWD in individual deer (state variable *cwdm*: duration from exposure to CWD-caused death). Infected deer surviving beyond this duration die (execute the CWD mortality submodel).

3. *CWD progression and transmission*

All infected deer execute *cwd-progression* schedule every time step. First, each infected deer updates the counter for CWD duration (*cwdpr* time since exposure in months). Deer in infectious phase (*cwdpr* > *cwdi* and *cwdpr* < *cwdc*) can transmit infectious prions to susceptible deer in their contact network. Although CWD can be transmitted indirectly (via environmental contamination), direct (animal-to-animal) transmission appears to be the dominant mechanism of disease spread in the early stages of CWD outbreak (Almberg, Cross, Johnson, Heisey, & Richards, 2011; Schauber, Nielsen, Kjær, Anderson, & Storm, 2015). In addition, management interventions can be more effective if implemented before CWD gets established in a population. In this model, only the direct (deer-to-deer) transmission mechanism is included.

Transmission is modeled using two probabilities: i) contact probability, specifically the probability of an infectious individual coming in contact with a susceptible individual, and ii) transmission probability, or the probability of infectious prion transmission given an infectious contact has occured. Contact probabilities are derived from the minimum and maximum number of contacts per time step specified for each age-sex class and group affiliation status in the user-specified contact matrix (contactstrucutre.csv). The transmission probability used in this model is derived using CWD prevalence data obtained from Wisconsin's endemic southwest core area between 2002 and 2008 (Kjær, 2010).

4. *Bachelor group formation*

Adult male deer are solitary during breeding season, but otherwise form temporary bachelor groups of nonrelated individuals (Hirth, 1977). 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 (Moore neighborhood); surviving group members from the previous year are recruited before new members. From second month up to ninth month, bachelor group leaders assess the group membership, and lose their leadership status if the group-size is less than 2. In the tenth month every year, bachelor groups break down for the rutting season.

5. *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).

a) Yearling male dispersal

Dispersal distances for yearling bucks are modeled using percent forest cover, as suggested by Diefenbach et al. (Diefenbach, Long, Rosenberry, Wallingford, & Smith, 2008). 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 (Long, Diefenbach, Rosenberry, Wallingford, & Grund, 2005)

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

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 (Diefenbach et al., 2008)

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

where *a* = 3.51 (SE = 0.597) and *b* = 0.77 (SE = 0.025). Dispersal distance (in kilometers) is obtained from a log-normal distribution using the predicted mean dispersal distance and predicted variance of dispersal distance (Diefenbach et al., 2008). The dispersal distance is then converted into miles, and the yearling male selects a random angle to disperse. 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.

b) 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 one of 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.

6. *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 (Ditchkoff, 2011). 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 with changed contact structure. 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 (Moore neighborhood) and adding up to two females along with their new-born fawns to the group.

7. *Mating*

Breeding interactions (courting rituals like flehmen behavior, tending and mounting) involve close contact between males and females, and could therefore facilitate CWD transmission. We assume that a mating interaction between a susceptible breeding female and an infectious breeding male results in up to five infectious contacts, and a mating interaction between a susceptible breeding male and an infectious breeding female results in five to 10 infectious contacts.

In the northern regions of United States, white-tailed deer breeding season is in the month of November (Ditchkoff, 2011). Bucks are sexually mature by 1.5 years of age, while does can attain sexual maturity as early as six months (Sorin, 2004; DeYoung et al., 2009; DeYoung & Miller, 2011; Turner, 2016). Younger males (1.5 – 2.5 years) make significant reproductive contributions, but older males are responsible for the majority of offspring (Sorin, 2004; DeYoung et al., 2009; Turner, 2016). Breeding males are known to increase their home range size during rutting season (Marchinton & Hirth, 1984). In this model, rutting period is simulated in the 11^{th} month each year, when mature bucks (> 2.5 years old) can mate with 1 to 6 breeding females in a radius of 1.5 miles, and young bucks (1.5 to 2.5 years old) can mate with 1 to 3 breeding females in a radius of 2.5 miles. Females of all age classes can participate in rutting behavior. Given the short and synchronized estrous period of 1-2 days when females are receptive (Hirth, 1977), and the nature of pre-breeding interactions like the formation of tending bonds by courting males, we assume that a breeding female interacts with at least one, and a maximum of 3 breeding males during the rutting season.

Table 2. Age- and sex-specific mortality parameter values derived from the regional deer harvest data (collected by DNR) and/ or expert opinions and calibrated for a typical agro-forested landscape of midwestern USA.

Parameter	Description	Value
Non-hunting mortality		
mf6nhm	male fawns (0 - 6 months)	0.065 per month [a]
ff6nhm	female fawns (0 - 6 months)	0.065 per month [a]
mf12nhm	male fawns (7 - 12 months)	0.07 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)	0.08 per year [c]
ff12hm	female fawns (7 - 12 months)	0.09 per year [c]
myhm	male yearlings (13 - 24 months)	0.47 per year [c]
fyhm	male yearlings (13 - 24 months)	0.22 per year [c]
mahm	male adults (> 25 months)	0.37 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 collected by Michigan Department of Natural Resources.

Parameterization and Calibration

Population dynamics of the model deer population is defined by two sets of age- and sex-specific parameters, hunting and non-hunting mortality rates. These parameters are imported along with the IN*Ov*POP-generated deer population snapshot. Hunting mortality rates are annual, while non-hunting mortality rates are monthly rates. The model interface has sliders to reset age-sex-specific hunting and non-hunting mortality rates. Realistic deer population snapshots for the desired region can be obtained by calibrating age-sex specific mortality parameters used in IN*Ov*POP.

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 (Nelson & Mech, 1992; B. F. Miller et al., 2010), but smaller group sizes (less than 8) are commonly seen in the Midwestern US, and bachelor group size typically ranges between 2 and 5 (Marchinton & Hirth, 1984; Smith, W, 1991; K. V. Miller, Muller, & Demarias, 2003), 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 (Gaillard, Festa-Blanchet, Yoccoz, Loison, & Toigo, 2000). 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% (Long et al., 2005) but predictive relationships are poorly understood (Diefenbach et al., 2008). 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% (Nixon et al., 2007). 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 (Lutz, Diefenbach, & Rosenberry, 2015).

Values for parameters *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 reporters.

The duration of CWD phases in infected deer are calibrated from published literature. In experimentally inoculated white-tailed deer, excretion of CWD prions has been documented as early as 6 months post-inoculation (Plummer, Wright, Johnson, Pedersen, & Samuel, 2017). Another study has documented a pre-clinical phase (from exposure to the onset of overt clinical signs) of 21 to 25 months in white-tailed deer orally inoculated with CWD prions (Johnson et al., 2011). In this model, pre-infectious phase is set between 6 and 10 months, pre-clinical phase between 21 and 25 months, and infected deer die within a month after they start exhibiting overt clinical signs of CWD. Therefore, the total course of CWD (from exposure to CWD-caused death) ranges between 21 and 26 months.

CWD is introduced in the model deer population in the sixth month of first year. User specifies the number and characteristics (age-sex class and group association) of deer that are initially infected (slider '*seed-infection*' and chooser '*CWD_introduced_by*' on the model interface). The following options are provided for CWD introduction: 1) adult deer, 2) dispersing male yearling, 3) dispersing female yearling, 4) group member doe, 5) solitary doe, 6) group member buck or 7) solitary buck.

The number of contacts (minimum-maximum per time step) between an infectious individual (first column) and susceptible individuals (columns 3 to 12) are provided in the contact matrix (contactstructure.csv). Seasonal fluctuations in the pattern and strength of social affiliations in white-tailed deer populations are considered while building the contact matrix (Table 4). Specifically,

1) The strongest associations within a doe social group are between females and their young and between sibling juveniles (Hawkins & Klimstra, 1970). Social interactions like allogrooming may play a role in CWD transmission as infectious deer shed

prions their saliva, urine and feces (Mathiason et al., 2006; Haley, Mathiason, Zabel, Telling, & Hoover, 2009; Tamgüney et al., 2009).

2) Newborn fawns have a close association with their mother as nursing occurs 2-6 times a day during the 1st month (Jackson, White, & Knowlton, 1972). We estimate a minimum of 60 and a maximum of 80 contacts over a month between a doe and her fawn of age one month or less. As the probability of transmission given an infectious contact is set at 0.0128 (Kjær, 2010), more than 80 infectious contacts per month results into a CWD transmission probability of 1. Full siblings bed separately during their first month, but start appearing together after they are a month old (Schwede, Hendrichs, & Wemmer, 1994). We do not simulate contacts between siblings less than a month old.
3) Fawns interact with siblings, and social play is common (Jacobson, 1994). Fawns are weaned when they are three months old (DeYoung & Miller, 2011). Post-weaning, male fawns associate less and more loosely with their mothers than female fawns (Schwede et al., 1994).
4) Doe social groups remain together year around except during the fawning season when parturient females isolate themselves (Hawkins & Klimstra, 1970; Nelson & Mech, 1981; Ozoga, Verme, & Bienz, 1982). Within group contact probabilities are high during the gestation period and low during the fawning season.
5) Between-group contact rates for does are estimated from Kjaer et al., 2008 (Kjær, Schauber, & Nielsen, 2008).
6) Yearling and adult bucks tend to be segregated from doe social groups except during the rutting season when courting males pursue and form tending bonds with receptive females (Smith, W, 1991; Kie & Bowyer, 1999). Except for the rutting season, bucks and yearlings occur in loosely associated bachelor groups (Hirth, 1977).

An important feature of IN*Ov*CWD is that the user can readily modify the contact matrix to incorporate updated information or alternate assumptions.

Table 3. Parameter values derived from peer-reviewed literature, field-based surveys or expert opinions for use in IN*Ov*POP and/or IN*Ov*CWD. An asterisk indicates calibrated values.

Parameter	Description	Value
Initial population setup and distribution		
PostHarvestDensity	Density of deer after the harvest season	14 per sq mile [a*]
sexratio	Female: male ratio in the population	1.5 [a]
adultprop	Proportion of adults (≥ 25 months) in the population	0.45 [a]
yearlingprop	Proportion of yearlings in the population	0.25 [a]
min%ForestCover	Minimum percent forest cover of deer habitat patch	0.25 (VerCauteren & Hygnstrom, 2004; Walter et al., 2009)
max%ForestCover	Maximum percent forest cover of deer habitat patch	0.75 *(VerCauteren & Hygnstrom, 2004; Walter et al., 2009)
Behavior		
mean-bachelor-group-size	mean (± standard deviation) number of adult male deer in a bachelor group	4 ± 1 [*](Marchinton & Hirth, 1984; Smith, W, 1991; K. V. Miller et al., 2003)
doe-group-size-regulator	group size (after fawning season) above which a doe social group undergoes fission	6 [*](Nelson & Mech, 1992; B. F. Miller et al., 2010) [b]
juvenile-pregnancy-rate	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 (Long et al., 2005; Diefenbach et al., 2008)
yearling-female-dispersal-rate	proportion of yearling females that disperse from their natal range	0.22 [*](Nixon et al., 2007)
mean-female-dispersal-distance	mean dispersal distance for yearling female deer	11 miles [*](Lutz et al., 2015)
stddev-dispersal-distance	standard deviation for the mean dispersal distance of yearling female deer	4 miles [*](Lutz et al., 2015)

[a] Derived from Michigan DNR's data.

[b] L. Hansen, pers.obs

[c] J. McRoberts, pers. Comm

Table 4.The dynamic contact pattern in INO*v*CWD is simulated using a contact matrix. The number of contacts per month (minimum-maximum) an infectious individual (first column) makes with susceptible deer (columns 3 to 12) are derived from the literature or expert opinions.

PERIOD	Age in months	MOM	FAWN(m)	FAWN(f)	FULLSIB(m)	FULLSIB(f)	NONSIB(m)	NONSIB(f)	GROUP(f)	NONGROUP(f)	BUCKS
GESTATION											
male fawn	9-12	5-10	0	0	10-20	5-10	10-20	5-10	0-5	0	0
female fawn	9-12	10-20	0	0	5-10	10-20	5-10	10-20	5-10	0-5	0
male yearling	21-24	0	0	0	0	0	0	0	0	0	1-5
female yearling	21-24	10-20	5-10	10-20	0	10-20	0	0	5-20	0-5	0
Buck	> 32	0	0	0	0	0	0	0	0	0	5-15
Doe	> 32	0-10	5-10	10-20	0	0	0	0	5-10	0-5	0
FAWNING											
male yearling	13-14	0	0	0	10-20	5-10*	10-20	5-10*	0	5-10*	0
female yearling	13-14 no fawns	0	0	0	5-10	10-20*	5-10	10-20*	5-10*	0	0
female yearling	13-14	0	60-90	60-90	0	0	0	0	0	0	0
Buck	> 26	0	0	0	0	0	0	0	0	0	5-15
Doe	> 26	0	60-90	60-90	0	0	0	0	0	0	0
Doe	25-26 no fawns	0	0	0	0	5-10*	0	0	5-10*	0	0
WEANING											
male fawn	3	60-90	0	0	60-90	60-90	0	0	5-10	0	0
female fawn	3	60-90	0	0	60-90	60-90	0	0	5-10	0	0
male yearling	15	0	0	0	0	0	0	0	0	0	1-5
female yearling	15	10-20	60-90	60-90	0	10-20	0	0	5-10	0-5	0
Buck	> 26	0	0	0	0	0	0	0	0	0	5-15
Doe	> 26	0-10	60-90	60-90	0	0	0	0	5-10	0-5	0
PRERUT											
male fawn	4-6	10-20	0	0	30-50	30-50	10-20	5-10	5-10	0	0
female fawn	4-6	20-30	0	0	30-50	30-50	5-10	20-30	10-20	0	0
male yearling	16-18	0	0	0	0	0	0	0	0	0	1-5
female yearling	16-18	10-20	10-20	20-30	0	10-20	0	0	5-10	0-5	0
Buck	> 28	0	0	0	0	0	0	0	0	0	5-15
Doe		0-10	10-20	20-30	0	0	0	0	5-10	0-5	0
RUT											
male fawn	7,8	0-5	0	0	10-20	0-5	10-20	0-5	0-5	0	0
female fawn	7,8	5-10	0	0	0-5	10-20	0-5	10-20	0-5	0	0-10
female yearling	19,20	0-5	0-5	5-10	0	0-5	0	0	5-10	5-8	0-15
Buck	> 15	0	0	0	0	0	0	0	0	0	0
Doe	> 26	0-5	0-5	5-10	0	0	0	0	0-5	5-8	5-30

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