

Appendix A. Overview, Design concepts, and Details protocol of the agent-based model used in this study

DeerLandscapeDisease: a spatially explicit agent-based model to assess transmission of chronic wasting disease in white-tailed deer (*Odocoileus virginianus*) populations

1. Purpose

The purpose of the DeerLandscapeDisease (DLD) model is to understand how different factors, such as landscape structure, movement, social behavior and transmission mode may affect disease transmission and resulting population-level prevalence and force-of-infection in white-tailed deer.

2. Entities, state variables, and scales

The model comprises four hierarchical levels: individual, landscape, time, and disease. Individuals are characterized by the state variables: identity number, age, sex, identity of the home range where the individual lives, group membership, and disease status. The animal model is built on a behavioral state principle. An animal is considered being in a specific state that is dependent on season, age, and sex of the animal. Certain behaviors or movement rules are then associated with a particular behavioral state, and transitions between states occur with certain events such as giving birth or mating. States in the model are: normal, dispersal, mating, and exploratory behavior. The model consists of three different agents: adult females, adult males and fawns. Each time step in the model is 2 hours, and aging of the agents is simulated in days, so on each new day (every 12th time step), every deer agent will have aged one day. The landscapes were created using 10x10 km maps of land cover for each study site described in the main manuscript (Fig. 1 in the main manuscript). We used 1997 and 2003 digital orthophoto quarter quadrangles (Illinois Geospatial Data Clearing

House, 2003) and ground-truthing to identify and delineate land cover types (Main manuscript, Table 1). The 10x10 km maps were converted to raster maps with square grid cells of 25x25 m, called pixels in ArcMap 10.6.1 (Environmental Systems Research Institute, 2017) and imported into Repast Symphony (North et al., 2007, 2005). In DLD, we refer to the southern Illinois landscape as the contiguous forest landscape, and the east-central Illinois landscape as the fragmented forest landscape. We used periodic boundaries (Topping et al., 2003) in our model landscapes.

2.1. Home range, grouping and fawn/doe relationship: Each adult deer in the model creates a home range based on field-recorded maximum and minimum home range sizes and on cover type percentages from field data (Appendix B, Table B1). Home range centers of different individuals cannot occupy the same pixel unless the individuals are related. If the animal is not able to establish a home range according to the criteria of home range size, no home range center overlap, and adequate forest cover, it will disperse. Fawns will only have their own home ranges if their mothers have died and left their home range to the fawn.

White-tailed deer form groups during most of the year. Males form loose bachelor groups except during the rut (Halls, 1984; Hirth, 1977; Marchington and Hirth, 1984; Nixon et al., 1994) whereas females form matriarchal groups, mainly with related individuals such as siblings or offspring (Nixon et al., 1991). Female groups tend to be quite stable (Nixon et al., 1991), but during parturition, pregnant does isolate themselves to give birth and rear their fawns (Hawkins and Klimstra, 1970; Nixon et al., 1992). For group movement within DLD, a leader is randomly chosen for each group. The leader moves independently, but each member of a group will then move with the leader at distances calculated from field data (See section 6). Females only form groups with related individuals (i.e. offspring, mothers, siblings). However, because we start out with no adult offspring at time zero in the model, females are allowed to group with unrelated individuals until

their first fawns turn into adults. We added this feature to simulate “normal” group and behavior dynamics from time 0. If an agent leaves a group, it is free to join another or the same group if all criteria for grouping are fulfilled (such as group size below maximum, relatedness for females etc). Sex-specific maximum group sizes can be found in Table B1 in Appendix B. To account for male groups being more fluid than female, we added a group adhesion parameter to the model. This adhesion parameter is the probability of staying within a group and is higher for females than males. However, during fawning, the adhesion value for females is zero, whereas it is zero for males during the rut (Appendix B, Table B1).

The first two months of a fawn’s life are mostly spent hiding and bedding down, waiting for the mother doe (Marchington and Hirth, 1984), so we modeled fawns less than 2 months of age to be sedentary. Each doe in the model visits its fawns 3 times a day during this period (at dawn, at midday, at dusk) to allow for potential nursing contacts. After 2 months, the fawns will follow their mothers until 1 year of age, where the fawn agent will turn into an adult (Section 2.2). If the mother of a fawn older than 2 months dies, the fawn will inherit the home range of its mother and move individually. The fawn will join the mother’s group (if the mother has one) as has been observed in nature (Woodson et al., 1980); this will happen regardless of siblings, and a fawn will only group with a sibling if the dying mom does not have a group. Seeing that a non-dispersing fawn will have the same home range center as its mother, related individuals will still be moving within the same home range.

If an animal cannot establish a home range, it will disperse. Furthermore, when a fawn turns into an adult it has a chance of dispersal of 70% for males and 20% for females (Appendix B, Table B1). These percentages lie within values reported for yearling dispersal for both agricultural and forested landscapes (Hawkins et al., 1971; Nixon et al., 2007, 1994; Rosenberry et al., 1999).

Most of the GPS-collared deer in our field study exhibited exploratory movements, usually during gestation and rut (unpublished data) and usually lasting <1 day (Schauber et al., 2007). Based on the observed frequency of excursions from our field data, we calculated average chances of exploratory behavior dependent on landscape and season for each individual deer (Appendix B, Table B1). Exploratory movement lasts between 12-24 hours, the duration being chosen randomly as the behavior starts, before the deer reverts to normal movements and returns to its home range.

2.2. Mating and Demographics: During the mating season (November 1 to December 31), males in the model search the surrounding area for females (search radius is 2 times the home range radius of the male. If the males does not have a home range, it is the maximum home range radius estimated for each landscape). When a male has found a non-mated female that is not being tended to by another male, the male follows the female for a random duration of 1-7 days before mating (Appendix B, Table B1, Marchington and Hirth, 1984). Once mated, a doe gives birth 187-222 days (randomly chosen) later (Marchington and Hirth, 1984) to 1 (0.25 probability), 2 (0.5), or 3 (0.25) fawns (Appendix B, Table B1). This distribution of litter sizes is based on literature (Verme and Ullrey, 1984) and to maintain a slowly-growing population in the model without density dependence or disease. We maintained a slowly-growing deer population, as harvest data from our study region in Wisconsin indicated a slow increase in the deer population during the period 1989-2001, where chronic wasting disease (CWD) was not present (Wisconsin Department of Natural Resources, 2012). At 1 year old, the fawn agent is replaced by an adult agent (50:50 sex ratio). The newly added adult agent retains fawn information, such as mother deer, ID, disease status and potential home range.

Because the model does not incorporate immigration or emigration, nor does it incorporate density dependence, mortality rates were adjusted within the published range to maintain a slowly

growing population when disease was not present as was observed in the study region (Wisconsin Department of Natural Resources, 2012). We used annual mortality rates of 0.4 for males and 0.2 for females (Appendix B, Table B1). These values lie within reported values for both agricultural landscapes (Nixon et al., 1994, 1991) and more forested landscapes (Hawkins et al., 1970; Nixon et al., 1994). We use annual mortality of 0.44 for fawns <2 months of age and 0.2 for fawns >2 months (Appendix B, Table B1). These values are a little higher than what Rohm et al. (2007) found, but necessary to maintain a slowly growing population within the model. Fawns are functional ruminants at 2 months old (Marchington and Hirth, 1984), so we assume that an older fawn could survive the death of its mother but a fawn <2 months old in the model dies if the mother dies.

2.3. Disease. We assume that a contact occurs if a deer occupies the same pixel as an infectious animal (direct) or pathogens deposited by an infected animal (indirect). Both direct infectivity and pathogen deposition rates are modeled as functions of time as is mortality caused by CWD (see section 6.2 and Appendix B, Table B2). Prions are persistent in the environment for at least several years (Bartelt-Hunt and Bartz, 2013; Smith et al., 2011; Williams et al., 2002). To model this, we assumed that the pool of available, infective pathogens declines exponentially after deposition in the environment with a half-life of 6 months (Appendix B, Table B2). This half-life is simply a starting point, as empirical data are lacking on how bioavailable environmental prion pools decay over time. Repeated visits to a pixel by infected animals cause prions to accumulate, so that the infectivity of a pixel is the sum of deposited prion infectivities.

Physical contact rates based on semi-hourly locations inherently are an imprecise reflection of a disease transmission process. A deer occupying a prion-contaminated pixel or a pixel with an infected deer at a given time step does not guarantee exposure and, alternatively, deer movement across such a pixel could also be missed by locations 2 hours apart. We accounted for

this imprecision by tuning the transmission parameters (probability of acquiring infection given direct or indirect contact) such that the model generated disease dynamics matching observed data. As the probability of infection given direct or indirect contact is unknown, we adjusted the probability of infection given contact so that prevalence in the model corresponded with adult female CWD prevalence in Wisconsin's endemic southwest core area (Samuel and Storm, 2016; Wisconsin Department of Natural Resources, 2012). We chose to use adult female prevalence, since fitting prevalence to all age and sex classes in the model was unfeasible, and adult females are the largest single group in white-tailed deer populations (Halls, 1984) and would largely be responsible for overall prevalence. Also, evidence seems to suggest that CWD transmission is directed from females to males and females to females (Gear et al., 2010), making females more important for CWD transmission. In Wisconsin, adult female prevalence increased from 0.042 in 2002 to ca. 0.072 in 2011 (Wisconsin Department of Natural Resources, 2012). To match this rise in adult female prevalence (females > 1.5 years of age), direct transmission scenarios were started with an overall prevalence of 0.04 whereas indirect scenarios were started with a prevalence of 0.047. We allowed for a higher starting prevalence in the indirect scenarios, since indirect transmission was a much slower process than direct transmission (Appendix B, Table B2). For both direct and indirect transmission scenarios, infected animals were set to have been infected 12 months prior to model start. We did this to allow the system time to get through transients dynamics before reaching the "year 0" adult female prevalence of ca. 0.042. When "year 0" was reached, we calibrated the models so that prevalence would increase by a factor of 1.715 in 10 years ($0.042 \times 1.715 = 0.072$). This calibration was assessed manually, constantly varying transmission coefficients and calculating prevalence all the while ensuring convergence of prevalence standard deviations. For both direct and indirect scenarios, the "burn in" period before "year 0" was reached was ≤ 6 years, and to avoid effects on general comparisons between scenarios, all statistical analyses omitted the first 5

years of model runs. Matching the Wisconsin rise in adult female prevalence in the contiguous forest landscape (this landscape resembling the Wisconsin endemic southwest core area landscape) yielded a chance of infection of 0.0218 for direct contacts and 8.235×10^{-6} for indirect contacts (Appendix B, Table B2, the value for indirect contact is lower, due to prion accumulation in the landscape). The same probabilities of infection given contact were used for the fragmented forest landscape to allow direct assessment of the effect of landscape structure. We assumed that infection probability given contact was equal for all age classes, and thus force of infection would depend on sex- and age-specific behavior leading to direct or indirect contacts.

3. Process overview and scheduling

Each time step in the model is 2 hours, the same time interval as the locations provided by most of the GPS collars in our field study. The following behaviors/behavioral phases are processed (dependent on season, age and sex) at each time step: disease status, mortality, home range status, grouping status, reproduction, fawn status (females only), mom status (fawns only), dispersal and exploratory behavior. Movement is a specific behavior that is dependent on the state of the agent. Individuals and their behavior/behavioral phases are processed in random order. The different behaviors/behavioral phases of males, females and fawns are depicted in Figure 2 in the main manuscript.

4. Design concepts

4.1. Basic principles: DLD focuses on white-tailed deer behavior and traits thought to affect disease transmission, both direct and indirect. Movement in particular, both individual and group movement, is thought to affect contact rates and thus potentially the transmission of disease from individual to individual or between the individual and the environment. Due to the importance of

movement in epizootiology, most of the movement rules and behaviors in DLD are based on empirical data, thus avoiding making assumptions that could affect model outcome. Therefore, movement is extensively modeled in DLD (see section 6). The disease component included in DLD is based on our current knowledge of CWD, and this knowledge is used to make predictions about prevalence levels in different landscapes and with different modes of transmission. However, because many factors are still unknown regarding CWD and the transmission modes and pathways, some assumptions had to be made in the model (see sections 2.3 and 6.4).

4.2. Emergence: Patterns of population dynamics and disease prevalence within the population emerge from the behaviors and fates of the individuals. The sections Adaptation, Learning, Objectives/Fitness and Prediction do not apply to DLD, since these behavioral traits are not explicitly modeled. However, traits such as adaptation and fitness may be implicitly modeled through the empirical probabilities and rules that represent the individual's fate and behavior - for example, mortality and dispersal rates are modeled as probabilities.

4.3. Sensing: In DLD, individuals have knowledge of their own sex, age, group members, offspring, landscape features, mother and time of year. This enables age- and sex-specific mortality probabilities, dispersal probabilities, grouping with related individuals (females), group adhesion probability, and the ability to establish home ranges based on cover types in the nearest vicinity.

4.4. Interaction: The agents in the model interact when being part of a group, when mating, and when females are caring for their fawns. The agents also interact with each other when transmitting CWD through direct contacts and with the landscape when depositing and encountering infective prions in the environment (indirect contact). Furthermore, the disease component of DLD interacts

with time: prion infectivity in the environment decreases with time, individual infectivity/prion shed rate increases as disease progresses, and disease mortality increase as the disease progresses.

4.5. Stochasticity: Most demographic and behavioral parameters in DLD are drawn from empirical probability distributions, or are probabilities. This was done to include demographic noise and to allow for stochastic effects to influence disease transmission in the two landscapes.

4.6. Collectives: The agents in DLD form social groups during most of the year. Females will form groups with related individuals, whereas males are less restrictive but will form groups with males in their vicinity (see section 2.1). Fawns have tight bonds with their mother during their first 6 months of life and their movements only allow little distance between mother and fawns. After their first 6 months, fawns will still stay with their mother, but distance between mother and fawn is more relaxed (see sections 2.1. and 6.3).

4.7. Observation: For model testing, the spatial distribution of the individuals, as well as grouping behavior was observed. For model analysis, both population-level and individual variables are recorded, such as population size over time, prevalence levels over time, as well as individual age, sex, disease status and group status.

5. Input, initialization and output

In order to obtain a measure of the starting population, we ran the model without the disease present to investigate the stable age and sex distribution between females, males and fawns. This resulted in a stable distribution ratio of 0.39:0.19:0.42 (females:males:fawns), and these proportions are used when starting the model. At the start of the model, fawns are randomly assigned to a mother after

the litter size distribution in Table B1 in Appendix B. Since the model starts 1. January, fawns at the start of the scenario runs are set to be 184 days of age (born on July 1st the previous year, which is approximately halfway through the fawning season). Starting population of animals comprises 1000 individuals distributed after the stable age and sex proportions described above, with CWD prevalences of 0.042 (direct transmission) and 0.047 (indirect transmission, see section 2.3.). To obtain these prevalences, CWD-positive status is randomly assigned to 42 and 47 individuals, respectively (Appendix B, Table B2). Following initialization, environmental conditions remain constant over space and time. DLD does not account for any modeled dynamic spatial heterogeneity and the only temporal heterogeneity modeled is through season-specific behaviors and disease progression, prion accumulation and environmental prion infectivity changing through time. Data output consists of csv files on summarized annual number of agents and number of infected agents, as well as annual files on each individual agent and their sex, age, location coordinates, grouping status and infection status (infected or not, time of infection). All data outputs are recorded on the first day of a new year, thus yearly prevalence is a snapshot in time, calculated both individually for each agent class and total over all agent classes as number of infected deer out of the total number of deer.

6. Submodels

6.1. Individual movement: To model individual movement and movement within a home range, we fitted different correlated random walk models (Appendix C, Fig. C1) to field-obtained semi-hourly GPS location data from each individual deer and season, maximizing likelihood using R.3.5.2 (R Development Core Team, 2018). We used the wrapped Cauchy distribution to model turn angle and the Weibull distribution to model step length (See Appendix C for details) and investigated 5 variants of the wrapped Cauchy model and 4 variants of the Weibull distribution to determine the

best fit to empirical movement data. For each variant we included distribution parameters where none, one or all of the parameters were functions of distance to the home range center. For details about modelling individual deer movement, see Appendix C.

6.2. Group movement: From empirical data, we calculated distance between group members at simultaneous locations and fitted season-specific exponential distributions to these distances (See Appendix C for details).

6.3. Fawn movement, mating movement, dispersal and exploratory movement: When modeling fawn movement, in order to ensure that fawn and mother stay close, distance vectors are drawn from an exponential distribution with a mean $\lambda = 0.1$ m until the fawn is 6 months old (Appendix B, Table B3). After the age of 6 months, the fawn will use the same distance distribution as for general group movement (see section 6.2). Both dispersal and exploratory movement are modeled with the same step lengths as normal movement but with a turn angle distribution concentrated around zero (Appendix B, Table B3) producing more linear paths. Because males are known to follow potential mates at close distances during the rut (Halls, 1984; Marchington and Hirth, 1984), the distance between the male and its prospective mate at each time step is drawn from an exponential distribution with $\lambda = 0.1$ m (Appendix B, Table B3).

6.4. Disease: Direct infectivity and pathogen deposition rates are modeled as functions of time using a Gaussian cumulative distribution function (CDF) with $\mu = 20$ months (latent period of 18 months + 2 months) and $\sigma = 4$ months (Appendix B, Table B2). This results in the diseased deer nearing maximum infectivity at 30 months post-infection, which is also the time where death due to disease approaches 100% (Williams et al., 2002). We included a latent period because CWD has an

incubation time before onset of clinical signs, although infectivity still seems to be present during the latent period (Belay et al., 2004; Williams et al., 2002). Mortality rates due to disease in the model also increased with time since first infected following a Gaussian CDF with $\mu = 28$ (latent period + 10 months) and $\sigma = 2$ months (Appendix B, Table B2). This way the animal will not have an increased mortality rate during the latent period, but mortality approaches 100% by 30 months since infection.

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