Model of pathogen transmission between livestock and white-tailed deer in fragmented agricultural and forest landscapes

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A B S T R A C T

The study summarizes the current knowledge on infection and recovery of white-tailed deer and cattle, and integrates this knowledge into the Soil and Water Assessment Tool (SWAT) via a new add-on module SIR (Susceptible - Infected - Recovered) for predicting pathogen transmission between livestock and deer. New processes modeled by the SWAT-SIR model include: (a) seasonal changes in deer population and habitat; (b) resource selection and seasonal changes in foliage consumption by deer; (c) ingestion of pathogens with water, foliage and via grooming soiled hide by deer and grazing cattle; (d) infection and recovery of deer and co-grazing cattle; (e) pathogen shedding by infected animals; (f) survival of pathogens in manure; (g) kinetic release of pathogens from applied manure and fecal material. The model output is linked with ARC-GIS to allow spatial and temporal analysis of pathogen distribution across the watershed for specific land use, weather and management scenarios. © 2016 Elsevier Ltd. All rights reserved.

Software and/or data availability

The SWAT-SIR module with example of SWAT ARC GIS project can be obtained from the first author upon request.

1. Introduction

Manure-borne pathogens such as Escherichia coli O157:H7, Salmonella, Campylobacter and Cryptosporidium have become a subject of growing concerns due to continuous water body impairment causing increased number of waterborne disease outbreaks in the United States and Canada (Besser et al., 1993; Cieslak et al., 1993; Jackson et al., 1998). In 2014, the U.S. Environmental Protection Agency reported 3451 impaired water bodies in the United States based on E. coli monitoring (U.S. EPA. 2014). Livestock is commonly considered among the major sources of fecal contamination (Jones, 1999; Chapman, 2000; Gallagher et al., 2012) with cattle as a principal reservoir of E. coli O157:H7 (Borzyn et al., 1987; Ørskov et al., 1987; Zhao et al., 1995). However, in fragmented agricultural and forest landscapes, wildlife can also serve as a reservoir for pathogens, thus contributing a considerable portion of the fecal pollution (Daszal et al., 2000; Ishii et al., 2007; Parajuli, 2007; Harmel et al., 2010). Several recent E. coli O157:H7 outbreaks were associated with deer. Specifically, 15 illness cases, including two deaths in Oregon in July—August 2011 were caused by strawberry-transmitted infection of E. coli O157:H7 produced by black-tailed deer (Laidler et al., 2013). Consumption of unpasteurized apple juice caused infection of at least seventy people by E. coli O157:H7 in the western United States and British Columbia, Canada, in October 1996. This outbreak of E. coli O157:H7 infection was suspected to be associated with apples coming from orchards frequented by deer (Cody et al., 1999). Since E. coli O157:H7 is spread via a fecal-oral route and both cattle and deer may harbor this pathogen, there is a possibility for the pathogen transmission between the two groups of animals through exposure to contaminated water and foliage (Branham et al., 2005). This possibility was supported by the results of Rice et al. (1995), Sargeant et al. (1999), and Renter et al. (2001) who isolated E. coli O157:H7 from feces of white-tailed deer co-grazing with cattle.

Multiple outbreaks associated with deer have prompted enhanced research of possible interaction and pathogen transmission between co-grazing domestic and wild animals (Rice et al., 1995; Sargeant et al., 1999; Renter et al., 2001; Daszal et al., 2000; Ishii et al., 2007; Parajuli, 2007; Harmel et al., 2010).
1995; Sargeant et al., 1999), Lejeune et al. (2001) showed that calves could become colonized with *E. coli* O157 after drinking from water sources that were fecally contaminated 183 days earlier. Branham et al. (2005) concluded that white-tailed deer could potentially become infected by *E. coli* O157:H7 and Salmonella spp. via consumption of water from cattle troughs, and conversely spread the pathogens to livestock and other wildlife. Modeling is commonly used to evaluate risk of surface water contamination by fecal bacteria. Several models have been recently used to predict fate and transport of manure-borne bacteria produced by livestock and wildlife at the watershed scale. For example, Hydrological Simulation Program—FORTRAN (HSFP) (Bicknell et al., 1997) was used to simulate total and source-specific contributions of fecal coliform bacteria to instream load from domestic and wild animals by Yagow et al. (2001), Moyer and Hyer (2003), Benham et al. (2006), Chin et al. (2009), and other studies. Soil and Water Assessment Tool (SWAT) (Sadeghi and Arnold, 2002; Neitsch et al., 2005) was used for bacteria source tracking by Baffaut and Benson (2003), Parajuli (2007), Parajuli et al. (2009), Coffey et al. (2010), Frey et al. (2013), and for predicting *E. coli* and fecal coliform concentrations in stream water by Baffaut and Sadeghi (2010); Kim et al. (2010), Cho et al. (2012), Ludicello and Chin (2013), and Jaydev et al. (2013). A relatively simple tool for bacteria source characterization, BSLC (Bacteria Source Load Calculator), was developed by Zeczkoski et al. (2005) to characterize the bacteria sources and loads for development of the TMDL (Total Maximum Daily Load) allocation scenarios. TMDL is a program established by U.S. Environment Protection Agency (EPA) in 1992 in response to Clean Water Act of 1972 describing the maximum amount of pollutants that a body of water can receive while still meeting water quality standards. Dorner et al. (2006) coupled a microbial fate and transport model with the WATFLOOD/SP9, a watershed hydrology modeling system, to determine the primary sources of pathogenic contamination in a watershed in Southwestern Ontario, Canada. Ferguson et al. (2007) developed a process-based mathematical model PCB (pathogen catchment budgets) to predict *Cryptosporidium*, *Giardia* and *E. coli* loads generated within and exported from drinking water catchments and applied this model for the Wingate creek catchment located approximately 200 km south west of Sydney, Australia. Park et al. (2014) recently extended the Agricultural Policy/Environmental eXtender (APEX) model to predict microbial fate and transport at farm and small watershed scales. Different approaches to modeling pathogen transport and risk assessment were further developed in an Integrated Environmental Modeling Framework (IEM) (Whelan et al., 2014).

Current microbial transport models were developed for indicator organisms of fecal contamination and bacterial impairment of watersheds. The most commonly tested fecal bacteria indicators such as total coliforms, fecal coliforms, *E. coli*, fecal streptococci, and enterococci are relatively harmless. They indicate possibility of presence of pathogenic microorganisms, though the concentrations of the pathogens themselves are generally unknown. To extend the existing models to predict pathogen transport and assessment of pathogen water contamination, the models must include the mechanisms and processes of pathogen transmission within the same groups of animals as well as between different groups. These mechanisms are not well studied and information about pathogen transmission between animals is scarce. Moreover, infection and pathogen shedding by domestic and wild animals depend on different environmental factors that are difficult to account for due to their high spatial and temporal variability. In this study we (i) summarized the current knowledge on infection and recovery of white-tailed deer and cattle, and (ii) integrated this knowledge into the SWAT model via a new add-on module SIR (Susceptible - Infected - Recovered) which can predict pathogen transmission between livestock and deer. We demonstrated the SWAT-SIR features that can be helpful for analyzing pathogen sources and for development of better management practices for reducing pathogen loads on fragmented agricultural and forest landscapes.

### 2. Materials and methods

#### 2.1. Theory

##### 2.1.1. Modeled processes and structure of the SIR module

As the basis for the development of our new SIR module, we used SWAT model. The SWAT software is frequently used to model bacteria fate and transport at a watershed scale, has a well-developed graphical user interface linked to ArcGIS (ESRI® ArcGIS™), and supports commonly used soil (SSURGO, NRCS) and land-use (NLCD2006) databases. Modified version of the SWAT2012 software (Kim et al., 2010) includes following bacterial processes:

- bacteria deposition on soil and foliage with applied manure or with fecal material of grazing animals;
- bacteria die-off/re-growth in soil, water and on foliage; bacteria wash-off from soil and foliage;
- bacteria leaching from soil; bacteria subsurface, overland and instream transport;
- bacteria deposition to and resuspension from streambed sediment.

This version of SWAT software was developed further to predict transmission of *E. coli* O157:H7 between livestock and grazing white-tailed deer. New add-on module SIR includes the processes shown in Fig. 1. A brief description of the modeled processes and SIR structure can be found in Guber et al. (2014). Here we present a complete description of the SIR module that includes governing equations, model parameters and simulation results.

Pathogens can be ingested by co-grazing cattle and deer with water, foliage and via grooming soiled hide and can cause animal infection (Fig. 1). The SIR module implements a dose—response approach to compute the probability of animal infection based on the ingested daily dose of pathogens. It is assumed that the infected animals shed pathogens at grazing areas in the amounts proportional to fecal material produced daily until their full recovery. The shed pathogens can grow, die-off in fecal material, and/or be

![Fig. 1. Mechanism of pathogen transmission in the Susceptible - Infected - Recovered (SIR) add-on module.](image-url)
released into the soil or on the foliage with rainfall water. The pathogens can also be washed off soil, manure and fecal deposits, and be transported further toward streams and rivers with runoff water. Microorganisms that survive in the bottom sediment can be resuspend during high flow events in streams and transported to tributaries of higher order. The resuspended pathogens and those that entered the streams with runoff water can be ingested by grazing animals in pathogen free areas and cause infection of healthy animals.

New processes that were integrated into the SWAT-SIR model to account for pathogen transmission between infected and healthy animals include:

- seasonal changes in deer population and habitat;
- resource selection and seasonal changes in foliage consumption by deer;
- ingestion of pathogens with water, foliage and via grooming soiled hide by deer and grazing cattle;
- infection and recovery of deer and co-grazing cattle;
- pathogen shedding by infected animals;
- survival of pathogens in manure;
- kinetic release of pathogens from applied manure and fecal material;

The processes listed above are modeled in the SIR module and then coupled with the processes simulated in SWAT2012 to compute the daily values of the following characteristics:

- number of infected deer and cattle;
- number of pathogenic and nonpathogenic cells ingested and shed by deer and co-grazing cattle;
- number of non-pathogenic and pathogenic cells in soil, on foliage and in runoff water;
- total number of non-pathogenic and pathogenic cells transported with overland and subsurface flow from each HRU to streams;
- instream concentrations of non-pathogenic and pathogenic cells.

The values of these characteristics are computed per unit area of hydrologic response units (HRUs) and sub-basins. An HRU is defined as a combined land area within the sub-basin represented by a unique combination of land cover, soil, and management features. While a sub-basin is defined as a group of HRUs bordering the same stream.

Stand-alone postprocessors transfer results of SWAT-SIR simulations to ASCII files for import to SWAT database for further spatial data analysis in ArcGIS. ASCII files generated by the postprocessors can also be used by any standard software supporting graphical analysis (e.g. MS Excel (Microsoft Co.), Sigma Plot (Systat Software, Inc.), or Grapher (Golden Software, Inc.).

2.1.2. Deer infection, recovery and population dynamics

Deer population is constantly changing across the year due to birth and mortality associated with accidents, predation, hunting, and diseases. These changes are modeled in the add-on SIR module separately for each sub-basin using forcing functions that accounts for deer birth (b), recruitments (r), and mortality (d) (Fig. 2). The population model coupled with a three-compartment SIR module (Keeling and Rohani, 2008) predicts deer infection and recovery. Infection of deer in the susceptible group (S) occurs through pathogen ingestion with water and foliage. Number of infected deer (I) is defined by the probability of the infection computed using a dose response-model. The infected deer recover at a daily rate d and constitute the recovered group (R), which is transitioned further to the group S at a daily rate w. The infected deer shed pathogens during the whole infection period at rates, which are specific for deer gender, age, season, and grazing conditions. The same approach is used to model infection and recovery of grazing cattle with parameters specific for this species.

The SIR module was applied for grazing cattle in a form:

\[
\begin{align*}
\frac{dS_c}{dt} &= -\beta_cS_c + w_f R_f \\
\frac{dI_c}{dt} &= \beta_cS_c - I_c \alpha_c \\
\frac{dR_c}{dt} &= \alpha_c I_c - R_c w_c
\end{align*}
\]

where index c denotes cattle; S, I and R are the abundance of susceptible, infected, and recovered animals, respectively, head ha\(^{-1}\); 1/\(\alpha\) is recovery period, days; \(\beta\) is infection rate, day\(^{-1}\); and 1/w is immune period, day.

For grazing deer, the SIR module was formulated for adults (a) and fawns (f) as:

\[
\begin{align*}
\frac{dS_a}{dt} &= -\beta_a^aS_a + w_f R_f \\
\frac{dI_a}{dt} &= \beta_a^aS_a - I_a \alpha_a \\
\frac{dR_a}{dt} &= \alpha_a I_a - R_a w_f
\end{align*}
\]

where index a denotes male (AM) or female (AF) adult deer, therefore the system of equations in the left part of Eq. (2) was used for both male and female adult deer; index f denotes fawns (FA); r is the recruitment rate, day\(^{-1}\); b is the birth rate, day\(^{-1}\); and d is the mortality rate, day\(^{-1}\).

The system of the first order differential Equation (2) can be reduced to a single equation to compute the changes in abundance of deer groups (AM, AF, FA) over the period of time \(dt\) as:

\[
\frac{d(AM + AF + FA)}{dt} = bFA - (d_{AM}AM + d_{AF}AF + d_{FA}FA)
\]

where parameters \(b, d_{AM}, d_{AF}\) and \(d_{FA}\) are defined using forcing functions that account for seasonal changes in deer birth and mortality (e.g., Altizer et al., 2006; Hosseini et al., 2004):
where $B$ denotes the height of birth function, day$^{-1}$; $c$ is a shape parameter controlling the steepness of the double-logistic birth function, day$^{-1}$; $SD$ is the start date for births, day; $d_1$ is the duration of parturition/recruitment, day; $d_2$ is the end date for post-parturition mortality of fawns, day; $M_b$ is the background mortality level (base height of mortality functions), day$^{-1}$; $M_f$ denotes the height of the fawn mortality function in spring-summer, day$^{-1}$; $M_w$ is the amplitude of winter mortality, day$^{-1}$; $D_w$ is the variance of winter mortality, day; $D_b$ is the variance of harvest mortality, day; $M_{wM}$, $M_{hAM}$, and $M_{hAM}$ are the harvests of day mortality for adult males, fawns, and females, respectively, day$^{-1}$.

Recruitment of white-tailed deer occurs in April, just prior to parturition, within a short period of time at a rate and partitioning between male and female computed as:

$$r = 1/[30(1 + \exp(c(SD - d_1 - t)))]$$

where $f_{AM} = 1/(1 + ratio)$ and $f_{AF} = 1 - f_{AM}$. The ratio is $b_{AM}/b_{AF}$.

2.1.3. Dose-response

The dose–response component of SIR module computes daily rates of cattle and deer infection by $E. coli$ O157:H7 based on daily values of pathogen ingestion by cattle and deer with water, foliage, and via grooming soiled hide. Two dose–response models commonly used for wildlife were implemented in this study (Haas et al., 2000): exponential model:

$$\beta = 1 - \exp(-dose/k)$$

where $\beta$ is the daily infection rate, day$^{-1}$; $D_{so}$ is the daily dose of $E. coli$ O157:H7 that infect 50% of the exposed population, CFU day$^{-1}$ head$^{-1}$; $a_{so}$ is the slope parameter; $dose$ is the number of pathogen cells ingested daily by cattle or deer, CFU day$^{-1}$ head$^{-1}$; and $k$ is the number of organisms that are ingested for one to survive and cause infection, CFU day$^{-1}$ head$^{-1}$.

Parameter $k$ in Eq. (6) was related to the parameter $D_{so}$ in Eq. (7) to simplify the data input for SIR module as:

$$k = -D_{so}/\ln(0.5)$$

Daily doses of $E. coli$ O157:H7 cells ingested by grazing cattle and deer were estimated based on the daily foliage and water consumptions, and on grooming soiled hide:

$$dose = C_{wat}V_{wat} + C_{fol}V_{fol} + C_{gsh}V_{gsh}$$

where $C_{wat}$, $C_{fol}$ and $C_{gsh}$ are $E. coli$ O157:H7 concentrations in water, on foliage, and on animal hide, respectively, CFU g$^{-1}$; $V_{wat}$, $V_{fol}$ and $V_{gsh}$ are mass of ingested water, dry forage and fecal material (i.e. grooming) daily by single animal, respectively, g day$^{-1}$ head$^{-1}$.

Daily water and foliage consumption for cattle is assumed to be time-invariant during the grazing period, but varied for deer with respect to age, sex, and season. To account for seasonal variation in water consumption by white-tailed deer fawns, does, and bucks we used the equations derived by Moen (1978) to relate deer weight to their age and day of the year:

$$M_{FAM} = 2.6 + 0.229A_{AF} \quad 0 < A_{AF} < 100 \quad M_{FAM} = \exp(1.617 + 0.381 \ln(A_{AF})) \quad A_{AF} > 100$$

$$M_{FAM} = 3.3 + 0.25A_{AF} \quad 0 < A_{AF} < 100 \quad M_{FAM} = 3.31A_{AF}^{0.4589} \quad 100 < A_{AF} \leq 260$$

$$M_{FAM} = 9.415A_{AF}^{0.3415} \quad \{0.83 + 0.17 \sin(0.9863J_{day} + 180)\} \quad A_{AF} > 260$$

where $M_{AM}$, $M_{AF}$, $M_{fAM}$ and $M_{fAF}$ are the weights of adult females, adult males, fawn females and fawn males, respectively, kg; $A_{AF}$ and $A_{AF}$ are the age of female and male fawns in days; $J_{day}$ is the day of the year. Since modeling the age of an individual deer at a watershed scale was impractical, the Moen’s equation was used for two deer gender groups in a simplified form:

$$M_{AF} = \overline{M}_{AF}\{0.9 + 0.1 \sin(0.9863J_{day} + 90)\}$$

$$M_{AM} = \overline{M}_{AM}\{0.83 + 0.17 \sin(0.9863J_{day} + 180)\}$$

where $\overline{M}_{AF}$ and $\overline{M}_{AM}$ are the average weights of adult females and males at $J_{day} = 365$. Then daily water consumption amount by individual deer was computed from deer weights $M_{deer}$ as:

$$V_{wat} = K_{wat}M_{deer}^{3/4}$$

where $K_{wat}$ is deer daily water consumption rate, g water per kg$^{3/4}$. Daily foliage consumption by deer relates to the seasonal deer metabolism and availability of the forage (Moen, 1978) as:

$$M_{fc} = \frac{mblm \cdot (70 \cdot 0.9 \cdot M_{deer})^{3/4}}{mefo}$$

$$M_{fol} = \frac{M_{fc} \cdot M_{fc} < M_{tol}}{M_{tol}}$$

$$M_{gsh} = \frac{M_{fol} \cdot M_{fol} > M_{tol}}{M_{tol}}$$

where $M_{fc}$ and $M_{tol}$ are the potential and available daily foliage consumption values by deer, g day$^{-1}$ head$^{-1}$; $mefo$ is the metabolize energy in the foliage, kcal g$^{-1}$; and $mblm$ is the baseline metabolism (kcal kg$^{-1}$ day$^{-1}$) computed as:

$$mblm = 1.0285 \cdot \sin(0.9863J_{day} + 239) + 2.6981$$

Grooming soiled hide has been shown to cause animal infections by smaller doses of $E. coli$ O157:H7 compared to the bacteria ingestion with water and foliage (McGee et al., 2004). Social grooming is common among the same and different deer sex groups (Miller; 1971; Forand and Marchinton, 1989), and therefore can cause the pathogen transmission from one individual to another. Ingestion of $E. coli$ O157:H7 via grooming was assumed.
where $D_{\text{doe}}$ is the total area of HRUs with k-land use in the sub-basin, ha; and $A_k$ is the total area with k-land use in the sub-basin, ha.

where $f_{\text{HRU}}^i$ is the probability that in a given $j$-month deer choose a HRU with k-land use for grazing; and $P_{\text{FRSD}}$ is the probability that in a given j-month deer choose a deciduous forest.

The sub-basins may consist of several HRUs with the same land use, but different soil types or terrain slopes. To account for fractions of the day that deer spend on each HRU of the same sub-basin, the probability values computed for each land use via Eq. (17) were normalized by the total area of HRUs with the same land use within one sub-basin as:

$$f_{\text{HRU}}^i = P_k^i A_{HRU}^i / A_k$$

where $A_{HRU}^i$ is the area of the i-HRU with k-land use in the sub-basin, ha; and $A_k$ is the total area with k-land use in the sub-basin, ha.
\[
C_{bac} = C_{bac}^{-1} \exp(-k_T dt) - C_{min}^{-1} \quad (22)
\]

where \( C_{bac} \) is the amount of bacteria present in the material (i.e. manure, soil, foliage, water) on a current day, CFU m\(^{-2}\); \( C_{bac}^{-1} \) is the amount of bacteria present on previous day, CFU m\(^{-2}\); \( C_{min}^{-1} \) is the minimum daily loss of bacteria for die-off, CFU m\(^{-2}\); \( dt \) is the time interval in SWAT simulations, 1 day by default; and \( k_T \) is the first-order rate coefficient for bacteria growth/die-off corrected for temperature as:

\[
k_T = k_{20} T^{-20} \quad (23)
\]

where \( T \) is the mean daily temperature (°C); \( \theta \) is the temperature correction coefficient; and \( k_{20} \) is the bacteria growth/die-off rate measured at temperature of 20°C (day\(^{-1}\)).

To describe bacteria release from applied manure and fecal material deposited by the grazing cattle and deer we used the Bradford-Schijven release model (Bradford and Schijven, 2002) in a form:

\[
M'_{bac} = E_M M_{bac}^{-1} \left(1 - \left(1 + a_{fcl} \beta_{fcl} \frac{Prec}{C_0} \right)^{-1}\right)^{-1} \quad (24)
\]

where \( M_{bac} \) is the number of bacteria cells released from fecal deposits into the aqueous phase on a current day, CFU; \( M'_{bac} \) is the number of bacteria cells in fecal deposits on previous day, CFU; \( E_M \) is the bacteria release efficiency, unitless; \( Prec \) is the daily precipitation, mm; \( a_{fcl} \) (mm\(^{-1}\)) and \( \beta_{fcl} \) (unitless) are the empirical parameters defining the shape of the release curve. The released bacteria are distributed between soil surface and vegetation proportionally to the vegetation density computed by the SWAT model.

### 2.2. Watershed description and simulation scenarios

#### 2.2.1. Watershed description

The add-on SIR module for the SWAT software was used to estimate the impact of \( E. coli \) O157:H7 transmission between livestock and white-tailed deer on the pathogen spread at a small watershed with fragmented agricultural and forest land uses. The land use within the 75.2 km\(^2\) watershed included forest (74%), hay (15.6%), and white-tailed deer on the pathogen spread at a small watershed.

#### 2.2.2. Parameters of the deer population component

The values of the parameters in Eqs. (3)–(4) were selected so as to provide the steady-state annual dynamics of the deer population. The seasonal variation in buck, doe and fawn quantities is accounted for, but the annual deer population is kept constant (Fig. 4). Fractions of different gender and age groups corresponding to these parameter values were 0.221, 0.428 and 0.351 for deer bucks, does and fawns, respectively. In the simulations we set the animal densities for grazing cattle to 4 head ha\(^{-1}\). Deer population dynamics is generally unknown. Bureau of Wildlife Management of Pennsylvania Game Commission use sex-age-kill model PASAK (Rosenberry et al., 2011) to monitor deer population trends. The model provides estimates of white-tailed deer population for 23 wildlife management units (WMU) for 2003–2009 years. To estimate deer density for the simulated watershed the deer densities were normalized by forest area for WMU 5A and then multiplied by forest area of the simulated watershed. Then deer abundance for January 1 2005 (0.14 head ha\(^{-1}\)) was estimated by fitting Eq. (2) and Eq. (3) to the PASAK-estimated values (Fig. 4).

Parameters of the forcing functions that account for the seasonal changes in deer birth and mortality (Eqs. (4) and (5)) were estimated from the literature. Birth rates for adult white-tailed deer vary from 0.67 to 2.27 fawns per female (DeYoung, 2011). Parturition of white-tailed deer in similar environments occurs during a short period of time (~3 weeks), with captive deer studies reporting births as early as May (Dechen Quinn, unpublished data) to mid June (Pekins et al., 1998). We fit a birth function that results in one fawn per female over the course of 20 days beginning 20 May: \( B = 0.05 \) day\(^{-1}\), \( c = 0.8 \) day\(^{-1}\), \( SD = 140 \) day, and \( d_1 = 20 \) day. White-tailed deer mortality is highly variable across their range and among sex and age classes (DeYoung, 2011).

We fit mortality functions with 7.5% winter-caused mortalities for all deer classes, 50% fawn mortality post-parturition, and class-specific mortalities due to fall harvest (fawns: 15%, adult females: 13%, and adult males: 38%): \( d_2 = 63 \) day, \( M_b = 10^{-6} \) day\(^{-1}\), \( M_m = 0.008 \) day\(^{-1}\), \( M_{mp} = 0.002 \) day\(^{-1}\), \( D_h = 15 \) day\(^{-1}\), \( D_m = 15 \) day\(^{-1}\), \( \mu_{fa} = 75 \) day, \( \mu_{fb} = 320 \) day, \( M_{ham} = 0.01 \) day\(^{-1}\), \( M_{mfa} = 0.0035 \) day\(^{-1}\), and \( M_{mfb} = 0.0004 \) day\(^{-1}\). The annual dynamics of deer birth, recruitment and mortality rates calculated using these parameter values are shown in Fig. 5. Fawn birth occurs in May and June, followed by fawn recruitment, while fawn death occurs, in June through August due to illness and predation, in October through December during hunting season and in March due to starvation. Hunting also causes high death rates for bucks and does in October through December.

The value of the ratio parameter for males and females born into the deer population in Eq. (5) was estimated based on Burke and Birch (1995) study. The authors analyzed offspring sex ratio of white-tailed deer during three sequential years in Michigan with respect to the maternal condition and age in total of 705 individuals and found that male to female ratio in newborn deer varied between 1.04 and 1.24 with average of 1.14. The infection rates for cattle and deer were computed using the dose–response models (description of parameter value estimations is provided below).

#### 2.2.3. Parameters of the dose–response and infection components

Values of parameters \( k, a_d \) and \( D_{so} \) for deer and cattle infection by \( E. coli \) O157:H7 are generally unknown and are found to vary greatly for other ruminants. For example, for pigs, Cornick and Helgerson (2004) estimated the \( k \) values for the enterohemorrhagic (EHEC) \( E. coli \) to be 4.59 \( 10^4 \) CFU. For rabbits, Haas et al. (2000) reported values of parameters in beta-Poisson model as \( D_{so} = 5.9 \times 10^4 \) CFU and \( a_{so} = 4.9 \). Value of \( k \) parameter computed for rabbits using Eq. (9) was 8.52 \( 10^5 \) CFU, that is two orders of magnitude higher than the value determined for pigs. The infective dose of \( E. coli \) O157:H7 for cattle varied from 2 to 10 log CFU in studies of Cray and Moon (1995), Cray et al. (1998), Sher et al. (2002), McGee et al. (2004) and likely was influenced by diet, microbial flora, animal age, and immune status (Cray and Moon, 1995; Zhao et al., 1995; Johnson et al., 1996; Hovde et al., 1999; McGee...
et al., 2004). For white-tailed deer the infective dose of 8 log CFU a nalidixic-acid resistant strain 86-24 Nal-R of \( E. \) coli \( O157:H7 \) has been reported by Fischer et al. (2001). Scarcity of data on the cattle and deer infection dose indicates the need in further research aimed at reducing uncertainty in estimation of these parameters.

For the software demonstration purpose of this study, the values of the parameter \( D_{50} \) were set equal to \( 5 \times 10^5 \) CFU day \(^{-1} \) head \(^{-1} \), while the values of the parameters \( a_d \) in the beta-Poisson model were set to be equal to 0.5 and 0.2 for cattle and deer, respectively. The other parameters related to the dose–response model were set for cattle as: \( V_{wat} = 60,000 \) ml day \(^{-1} \) head \(^{-1} \).

\[ M_{rat} = 22.7 \text{ kg day}^{-1} \text{ head}^{-1} \] (Redfearn and Bidwell, PSS-2871); and for the deer: \( M_{JAM} = 118 \) kg, \( M_{JAF} = 77 \) kg, \( 70(\text{dec-gefo-meco}) = 0.0301, K_{wat} = 118 \) ml water per kg\(^{3/4} \) (French et al., 1956; Ullrey et al., 1968, 1970; Moen, 1978; Lautier et al., 1988). Annual dynamics of deer weight, consumption of foliage and water calculated using Eqs. 11–13 and these parameter values are shown in Fig. 6.

2.2.4. Parameters of the resource selection component

The odds ratios were estimated based on monitoring data obtained using GPS collared white-tailed deer in central NY (Dechen Quinn et al., 2009). GPS collars acquired a location every 5 h and collars were remotely detached and retrieved after approximately 1 year. All deer were captured and handled in accordance with protocols approved by the Institutional Animal Care and Use.
Committee at the State University of New York College of Environmental Science and Forestry (protocol no: 2005-1). We incorporated a use-versus-availability design structure to determine relative probability of selection of various resources by white-tailed deer (Boyce et al., 2002; Manly et al., 2002) and defined the domain of available habitat using a step selection function similar to that employed in Fortin et al. (2005) using R 2.15.2 (R Development Core Team 2012). For each GPS location observed at time (t), we sampled randomly from an empirically derived exponential distribution of step lengths (distance between two GPS locations) and a von Mises distribution of turn angles (direction of travel between two GPS locations). Each step length/turn angle pair originated at the observed point (t) and generated a random point on the landscape. Then five random points for each GPS location were produced and each random point generated from (t) was compared to the used location at time (t+1). In this way, we were able to compare step-specific availability at (t) to what the animal actually selected at (t+1). Available points were considered random, but conditional on the location of the observed point from which they were generated. Landscape attributes were extracted from 30 × 30 m resolution raster layers to each corresponding observed or available location in ArcGIS 10.0 (ESRI 1999–2010). Land cover type was recorded as a categorical variable; distance to water as a continuous variable. Land cover identification was determined from the 2006 National Land Cover Database (Fry et al., 2011) that we reclassified from 21 land cover categories to 9 categories of the Anderson classification system: open water, urban land, coniferous forest, mixed forest, hay, row crops, rangeland, and wetland (Anderson et al., 1972). The reclassified land cover categories were used to elucidate the functional differences between forage and cover that were presumed to be important in driving space use by white-tailed deer while presenting a parsimonious model that reflected reasonable statistical power.

A surface that calculated continuous, Euclidian distance from hydrological features to the deer location was generated for the watershed used in this study. This variable evaluated their distance to water features, such as streams and drainages. It is distinguished from the land-cover type ‘open water’, which is typified by larger bodies of water. We developed candidate models that reflected these variables hypothesized to serve as important resources to white-tailed deer and used a conditional logistic regression within the Cox Proportional Hazards (coxph) function from the survival package (Therneau and Lumley, 2009) in R 2.15.2 (R Development Core Team 2012). To obtain odds ratios we divided the dataset into monthly subsets and fit the same set of models to each monthly subset:

$$\logit\left(P_k^j\right) = \beta_0^j + \sum_{k=1}^{n} \beta_j^k X_{k}^{j} \quad n = 8 \quad j = 1 - 12 \quad (25)$$

where $X_{k}^{j}$ is categorical variable for $k$-land use; $k$ is the land cover index; $j$ stands for month of the year; $\beta_j^k$ are log(OR$^j_k$). Average monthly values of odds ratios OR$^j_k$ for different land uses are shown in Table 1 of Appendix B.

2.2.5. Parameters of the recovery and pathogen shedding components

The recovery periods $1/\alpha$ for cattle and deer were estimated from Sanderson et al. (1999), Khaitza et al. (2003) and Fischer et al. (2001). Sanderson et al. (1999) studied fecal shedding of E. coli O157:H7 by one-week-old calves orally inoculated with 5·10^8 CFU of E. coli O157:H7 that was a nalidixic-acid resistant strain 86-24 Nal-R. The authors showed that following the first inoculation, the calves shed E. coli O157:H7 in their feces for 20–43 days, and the E. coli O157:H7 shedding period decreased to 3–8 days after the second and third inoculations. Khaitza et al. (2003) found for
feedlot cattle that the duration of \( E. \text{coli } O157:H7 \) shedding varied from 2 to 4 days during pre-epidemic period, from 21 to 30 days during epidemic, and from 4 to 14 days in post-epidemic period. \cite{Fischer01} investigated fecal shedding of \( E. \text{coli } O157:H7 \) by deer that received \( 10^9 \) CFU inoculum of nalidixic acid-resistant strain. The authors found that deer can shed \( E. \text{coli } O157:H7 \) up to 26 days post inoculation, (DPI) with maximum \( E. \text{coli } O157:H7 \) concentrations in deer feces from 3.5 to 5.1 log10 CFU during the first 10 DPI followed by a decrease to less than 10 CFU of \( E. \text{coli } O157:H7 \) per gram of feces during 12–17 DPI.

Simulation of infection and recovery of individual animals is impractical at a watershed scale since their exact grazing area is generally unknown. In this study we assumed, therefore, that all infected animals shed the same number of \( E. \text{coli } O157:H7 \) cell per gram of feces during the whole recovering period of time. The recovery periods and shedding \( E. \text{coli } O157:H7 \) concentrations were estimated from linear parts of the cumulative curves of \( E. \text{coli } O157:H7 \) cells shed by cattle and deer as a function of time. These curves were generated for cattle based on the results of \cite{Sanderson99} and for deer based on the results of \cite{Fischer01} (Fig. 7). We first computed the slopes of the cumulative curves, that are time averaged \( E. \text{coli } O157:H7 \) concentrations in feces of infected animals, and then calculated recovery periods dividing the total number of \( E. \text{coli } O157:H7 \) cells shed during the infection period by the slope of the cumulative curves. The mean values of the recovery periods are shown for deer and cattle in Table 2 of Appendix B. Concentrations of nonpathogenic \( E. \text{coli } \) in cattle and deer feces in this table were set based on \cite{Soupir06} and \cite{Guber15} studies.

Seasonal values of deer defecation rates were estimated from \cite{Rogers87} publication, who reported seasonal variation in the number of fecal pellet groups deposited daily by seven free-ranging female white-tailed deer in mixed coniferous-deciduous forests in northeastern Minnesota (Table 3 of Appendix B). The same study reported that the number of pellets in groups ranged from 30 to 96 with an average of 68.7 pellets group\(^{-1}\). Dry weight of a deer pellet was set equal to 0.214 \( \pm \) 0.056 g pellet\(^{-1}\) based on our direct measurements. The seasonal variability in cattle defecation rates was ignored in simulations and the daily rates were taken from ASAE D384.2 publication.

Fig. 8 illustrates seasonal variation in deer defecation rates calculated for does, fawns, and bucks using Eq. (19) and parameter values adjusted for bucks and fawns using Eq. (20). It can be seen in Fig. 8, that minimum and maximum defecation rates for all deer groups corresponded to Winter and Fall, respectively, while the intermediate defecation rates occurred in Spring and Summer months.

There are a few studies that reported an immune response of deer and cattle to infection by \( E. \text{coli } O157:H7 \). No antibodies against \( E. \text{coli } O157:H7 \) were detected in exposed deer in \cite{Fischer01}; that lack of detection was attributed to minimal interaction between the bacteria and the host. The calves reinfected by 10 log CFU of \( E. \text{coli } O157:H7 \) 13–14 weeks after the last positive fecal sample were all reinfected in \cite{Cravy95} study. However, after the first inoculation the calves shed considerably longer and higher \( E. \text{coli } O157:H7 \) concentrations than after subsequent reinoculation. The calves which were positive for 14 and 20 weeks after primary inoculation were positive for 4 and 3 weeks after reinoculation. No or little change in \( O157 \) antibody titers in calves administered \( 10^9 \) and \( 10^7 \) CFU were found in \cite{Johnson96} and \cite{Shere02} studies. The first study also revealed changes in the antibody titers at \( E. \text{coli } O157:H7 \) inoculation dose of \( 10^{10} \) CFU, however the antibodies did not influence the reinfection of the animals with the same \( E. \text{coli } \) strain. Based on the results of these studies, the value of the immune period parameter \( 1/\mu \) was set equal to 1 day meaning that all recovered animals (R) transferred to the susceptible group (S) on the first day after their recovery.

### 2.2.6. Bacteria survival and release parameters

Parameters of the Chick's first order decay Equation (22) and Arrhenius temperature correction Equation (23) were estimated based on the \( E. \text{coli } \) die-off kinetics or the kinetics parameters measured by different authors in soil, bottom sediment, animal feces, dry manure, and manure slurry for different temperature ranges (Fig. 9). Part of this dataset was obtained in \( E. \text{coli } O157:H7 \) studies and therefore should describe more accurately the pathogen survival compared to the other \( E. \text{coli } \) strains. Due to limited published data on the pathogens, the parameters summarized in Table 4 of Appendix B were applied for both pathogenic and nonpathogenic \( E. \text{coli } \) strains in SWAT-SIR simulations of this study.

Parameters of the Bradford-Schijven bacteria release model

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![Fig. 7](image-url) Cumulative amounts of \( E. \text{coli } O157:H7 \) shed in cattle and deer feces calculated based on \cite{Sanderson99} and \cite{Fischer01} studies, respectively. Different symbols denote values measured for individual animals; lines denote regression models fit to the linear part of the curves.
(24)) adopted from Guber et al. (2015) publication are shown in Table 5 of Appendix B. Fig. 10 illustrates the release kinetics of bacteria from four different fecal materials as a function of precipitation computed based on the parameter values shown in Table 5 (Appendix B). The release is the fastest from liquid manure, followed by fresh manure and deer feces with solid manure being the lowest.

### 2.2.7. Simulation scenarios

Pathogen transmission between co-grazing cattle and deer was evaluated in three simulation scenarios. The same management practices, weather conditions, duration and conditions of grazing, animal population dynamics, and resource selection parameters were used in all three scenarios.

The scenarios differed in E. coli O157:H7 content in the applied manure and in the initial number of infected cattle, and the specific settings used in the three scenarios are shown in Table 1. Specifically, in scenario 1, 4% of cattle were infected by E. coli O157:H7 in the beginning of grazing season while the applied manure contained no E. coli O157:H7. In scenario 2, the cattle was not infected by E. coli O157:H7 in the beginning of grazing season, however the applied manure contained E. coli O157:H7 in amount of $1.11 \times 10^3$ CFU (g dry mass)$^{-1}$. In scenario 3, both cattle infection by E. coli O157:H7 and application of manure with E. coli O157:H7 were present. Whole deer population was not infected in the beginning of the simulations in either of the studied scenarios (January 1st).

We ran the SWAT-SIR model with values of the hydrological parameters obtained by Kim et al. (2010) using SWAT calibration on water hydrograph data and concentrations of E. coli measured in steam at monitoring location shown in Fig. 3. Manure production by cattle was set equal to 51, and 68 wet kg day$^{-1}$ head$^{-1}$ for beef and lactating cows (American Society of Agricultural Engineers (ASAE) D384.2), respectively. Average water content of the manure was estimated as 86% (ASAE D384.2). E. coli concentrations in the liquid manure applied from an aerobic digester were reduced by 0.5 log factor compared to fresh cattle deposits (CH2M Gore & Storrie Limited (CG&S), 2000; Daigger and Bailey, 2000). The manure was applied on pastures and hay fields on May 8th. The application rates

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**Fig. 8.** Seasonal changes in defecation rates for three deer groups.

**Fig. 9.** Relationships between E. coli die-off rates and temperature estimated for different environments based on the parameters of the E. coli inactivation model obtained from published studies listed in Table 5 of Appendix B. Symbols denote measured data, while lines denote the values computed using Eqs. (22) and (23).

**Fig. 10.** Release kinetics of E. coli from manure and deer feces.
were 47.8 ton ha$^{-1}$, 3.0 ton ha$^{-1}$ and 14 ton ha$^{-1}$ for the solid manure at hay, liquid manure at hay and solid manure at pastures, respectively. Cattle grazing season at pastures started May 24 and lasted 150 days. The simulations were conducted for one year with precipitation and temperature shown in Fig. 11.

3. Uncertainty analysis

Uncertainty analysis was conducted to evaluate the relative impacts of input variable uncertainties on model prediction uncertainty for the three simulation scenarios shown in Table 1. A comprehensive review of uncertainty evaluation methods for deterministic models in environmental modeling can be found in Hammonds et al. (1994), Refsgaard et al. (2007), Matott et al. (2009). Specifically for SWAT, Talebizadeh et al. (2010) evaluated uncertainty in predicting sediment loads associated with the uncertainty of soil erodibility and hydraulic properties. Uncertainty was quantified using a 95% confidence interval of the predicted variable, and $p$- and $d$-factors as described by Abbaspour et al. (2004). The $p$-factor indicated the percentage of observations bracketed by the 95% confidence interval of the predicted variable, while the $d$-factor was the average width of the 95% confidence interval normalized by the standard deviation of observed values. The same statistics with little variation were used by Setegn et al. (2010), Shen et al. (2012), Singh et al. (2014), and Leta et al. (2015) to evaluate uncertainty in predicted streamflow associated with rainfall uncertainty and parameters of overland and groundwater flow. Zhang et al. (2009) used 66.7% and 90% confidence intervals to evaluate uncertainty in predicted streamflow.

The analysis of model predictive uncertainty associated with parameter uncertainty assumes that the model is calibrated, validated and probability distributions of the input model parameters are known. In this study due to absence of measurements on deer and cattle infection rates, model calibration and validation was not possible. Therefore, we relied on parameters of deer and cattle infection components estimated from limited literature data. We also expected interactions between different parameters of the SIR module to affect predictive uncertainty, however these interactions were generally unknown and therefore difficult to account for in the uncertainty analysis. For these reasons a comprehensive analysis of the effect of parameter uncertainty on model predictive uncertainty using methods of uncertainty analysis commonly used in hydrological modeling (e.g., Beven and Binley, 1992; Thyer et al., 2009; Vrugt et al., 2003; Leta et al., 2015) and statistics implemented for SWAT in the listed above publications was not possible for the SIR module. We instead used a simplified uncertainty analysis in this study. In performing such an analysis, we anticipated that even a simplified uncertainty analysis of pathogen transmission between wildlife and domestic animals would provide new insights into fate and transport of pathogens in mixed forest-agricultural settings and stimulate new research in this area. In this sense we agree with Jakeman et al. (2006) that “...improvement of understanding of the system is almost always a purpose of modelling ...” and “It is important to recognize that some purposes, particularly increased understanding of the system and data, may be realised well even if the final model is poor in many respects. An inaccurate model may still throw light on how an environmental system works”. We also used the interquartile range (a 50% confidence interval) instead of a 95% confidence interval to characterize the predictive uncertainty of the percentage of infected co-grazing deer and cattle, and E. coli O157:H7 contents in applied manure and fecal deposits of deer and cattle. Similar to the 95% confidence interval in surface hydrological modeling, the interquartile range is commonly used to quantify a spread of diseases in epidemiology (Merrill, 2009; US-HHS, 2006). Prediction uncertainty was also quantified using variance of the percentage of infected cattle and deer (Bennett et al., 2013).

Nineteen model parameters representing four components of the SIR module were selected for the uncertainty analysis (Table 2 of Appendix B). To reduce the number of model runs we used the Latin hypercube sampling (LHS) approach with mean and standard deviation values shown in Table 2 of Appendix B. The standard deviation values corresponded to a coefficient of variation equal to CV = 5% for all model parameters except the parameter $a_d$ in the dose–response component, where CV was set to 25% due to relatively low model sensitivity to this parameter compared to the others. Parameter values were assumed to be normally distributed and constrained by 90% confidence intervals of their values to exclude extreme parameter values.

Special attention was paid to the parameters of the resource selection component. It was impractical to generate 84 parameters representing all 7 land uses for all 12 months. The differences in variation of $\ln(\text{OR}_k)$ were not statistically significant over 12 months within each land use but were significant for land uses. Therefore, we generated the values of $\ln(\text{OR}_k)$ using a normal distribution with zero mean and monthly averaged $\sigma$ values separately for each land use (Table 2 of Appendix B). Then the odds ratios were calculated individually for each month and land use as:

\[ \text{OR}_k = \exp(\mu_k + \sigma_k), \]

where $\mu_k$ is the mean of $\ln(\text{OR}_k)$ for the $k$th land use and $\sigma_k$ is the standard deviation of $\ln(\text{OR}_k)$ for the $k$th land use.
\[ OR^k_j = \exp \left( \ln \left( OR^k_j \right) + \sigma_k \right) \]  

(26)

where \( OR^k_j \) is average monthly odds ratios for \( j \)-month and \( k \)-land use, \( \sigma_k \) is the standard deviation of \( \ln(OR^k_j) \) for \( k \)-land use.

The UNIX Library/Standalone version of the Latin Hypercube Sampling Software (Swiler and Wyss, 2004) was used to generate the parameter dataset for the SWAT-SIR uncertainty analysis.

4. Results

The developed SWAT-SIR software allowed analyzing annual dynamics of deer and cattle infection and spatial distributions of total \( E. coli \) and \( E. coli \) O157:H7 loads across the watershed. The annual dynamics predicted in the three scenarios indicated a possibility of deer and cattle infection via consumption of foliage contaminated by \( E. coli \) O157:H7, which was applied with manure or shed by infected cattle. Up to 1.5% of deer were infected soon after application of dry manure, which contained \( E. coli \) O157:H7 in May (Fig. 12b,c), however deer infection did not occur in May in the first scenario, where the manure was not applied (Fig. 12a). The manure application did not affect the grazing cattle. By the beginning of the cattle grazing period, the \( E. coli \) O157:H7 content in the manure decreased to such levels that caused infection only in 0.1% of the cattle population (Fig. 12b). The model predicted deer infection in July through November in the scenarios where 4% of the cattle was infected by \( E. coli \) O157:H7 in the beginning of the grazing season (Fig. 12ac). The percentage of the infected deer followed the increase in the number of co-grazing infected cattle, the increases typically occurred after intensive rainfalls. The maximum percentage of the deer infected by co-grazing cattle reached 0.5% that was less compared with the number of infected deer caused by the manure application. The relatively small number of infected deer in August–October compared with May in

![Fig. 12. Percentage (a–c) and variance (d) of infected cattle and deer populations obtained in the three simulation scenarios. Solid, dotted and dash lines (d) denote variance values for scenarios (a), (b) and (c) as, respectively.](image-url)
scenarios 1 and 3 (Fig. 12a,c) can be explained by overall smaller loads of *E. coli* O157:H7 with cattle fecal material compared to the solid manure.

The infection periods and the numbers of infected animals differed in the three studied scenarios and depended on the source of the infection. The first infection affected approximately 1.5% of the deer population and the infection period lasted approximately 2 weeks, that was twice as long as the deer recovery period 1/α (Table 2 of Appendix B). The long infection period and the shapes of the curves in Fig. 12b and c implied that *E. coli* O157:H7 survived in the applied manure and was released from it on foliage at the pasture during multiple rainfalls in May–June, causing several deer infection events.

We have not seen a noticeable *E. coli* O157:H7 transmission from deer to cattle in the simulations. The maximum *E. coli* O157:H7 content in deer feces deposited on pasture did not exceed 10 CFU m<sup>-2</sup> in the simulations. This can be partly attributed to spatial averaging of *E. coli* O157:H7 content at HRUs by the model, which probably resulted in smaller bacteria contents per unit area than those that could be expected in reality. However, the main causes of the absence of the *E. coli* O157:H7 transmission were small deer population (14–21 heads per 100 ha of forest area), foliage availability in non-contaminated agricultural lands, and relatively small fecal mass produced by deer, which was dispersed across large grazing area.

The uncertainty analysis revealed high variations in numbers of infected deer and cattle in simulations with parameters generated at CV = 5%. The variability in numbers of infected animals increased with the increase in overall numbers of infected animals; the highest interquartile ranges and variance were 2% and 3.7% for cattle, and 0.8% and 1.7% for deer at average percentage of infected animals of 1.8% and 1.0% for cattle and deer, respectively (Fig. 12). The high uncertainty of the model predictions was likely caused by high model sensitivity to the parameters, particularly to the dosage and bacteria shedding components, in the simulated scenarios. A comprehensive model sensitivity analysis to the parameters introduced in the four new model components as a function of weather and management scenarios is beyond the scope of this publication, and will be the subject of future model experiments and development.

The uncertainty in *E. coli* O157:H7 concentrations predicted in manure and fecal deposits, assessed as the interquartile range (Fig. 12a,b,c) and variance (Fig. 12d), increased with the time. The uncertainty was the lowest before the start of cattle grazing season and the highest at the end of the season. The low uncertainty obtained in the simulations was attributed to relatively small pathogen production by deer compared to the production by cattle. Average daily production of *E. coli* O157:H7 were 9.3·10<sup>6</sup> CFU head<sup>-1</sup> and 5.6·10<sup>7</sup> CFU head<sup>-1</sup> by infected deer and cattle in simulated scenarios, respectively. Moreover, infected deer spent only fraction of day on pasture that considerably reduced their pathogen loads on pastures. The high uncertainty in *E. coli* O157:H7 concentrations was associated mostly with uncertainty of the parameters for grazing cattle. It can be seen in Fig. 12a and c that the values and uncertainties in the *E. coli* O157:H7 concentrations were approximately the same during grazing season despite of the differences in percentage of infected deer and manure application scenarios. Both deer and applied manure had little effect on the *E. coli* O157:H7 during grazing season. This occurred due to relatively low pathogen input from deer on one hand, and considerable decrease of pathogens resided in the applied manure on other hand, that reduced *E. coli* O157:H7 contents in the fecal material below 25 CFU g<sup>-1</sup> (Fig. 12b). This pathogen level was by far below the infection dose for both deer and cattle.

The uncertainty patterns in percentage of the infected cattle followed the uncertainty in the *E. coli* O157:H7 content in fecal deposits in scenarios 1 and 3 only until mid of August (Fig 12a,c,d). Further increase in the deposited pathogen contents coincided in time with the decrease in percentage of infected cattle. The differences in the uncertainty patterns were partly attributed to the decrease in percentage of infected cattle due to recovery and to a small number of rainfall events in September and October. Low
precipitation considerably reduced release of pathogens from cattle deposits on foliage, and as a result reduced probability of cattle infection. The observed patterns could be specific for the simulated scenarios, and open an interesting avenue for further model exploration.

Examples of spatial distributions of E. coli loads by deer and from livestock operations obtained in the simulated scenario 3 are shown in Fig. 13. High spatial variability in the distribution of E. coli across a relatively small watershed was attributed to different land use and management practices. Less total E. coli cells transported with runoff from forested areas and more from pastures resulted in higher E. coli loads on surface water where pastureslands dominated in sub-basin area (Fig. 13a). Despite the relatively large area occupied by forests, the contribution of deer to the total E. coli loads on the surface waters was 2–3 orders of magnitude smaller compared with the loads from the livestock operations and particularly grazing. E. coli O157:H7 runoff patterns (Fig. 13b) resembled spatial distribution of total E. coli, however the absolute values for E. coli O157:H7 were two orders of magnitude smaller than those for E. coli. Fig. 13c and d illustrates simulated loads of E. coli O157:H7 on HRUs from livestock operations and by infected deer. It can be seen that despite smaller E. coli O157:H7 numbers, the area where the pathogens were spread by deer considerably exceeds the area where the pathogens were applied with manure or shed by the infected cattle. E. coli O157:H7 in amounts 10–100 CFU m-2 were spread by deer to the bay fields bordering the infected pastures. These results were obtained for the scenario when only 2% of deer population shed the pathogens, and the E. coli O157:H7 amounts could be considerably higher under the scenario with a larger percentage of infected deer.

The software developed and the results obtained in the simulations open a broad avenue for further research of the pathogen transmission between livestock and wildlife, which potentially can be extended to different domestic and wildlife species.

5. Conclusions

A new add-on module SIR developed for the watershed scale model SWAT can predict transmission of the manure-borne pathogens between livestock and deer. The new model allows analyzing annual dynamics of infected cattle and deer, pathogen shedding and loads on agricultural and forested lands, release of pathogens from fecal deposits to foliage and soil, pathogen overland transport and surface water pollution. The software provides insights into relationships between farm manure operations, pathogen transmission to deer, and pathogen appearance in surface water. This information can be helpful in identifying the potential sources of pathogenic microorganisms and for development of better management practices to reduce pathogen loads on fragmented agricultural and forest landscapes.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.envsoft.2016.02.024.

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198 A.K. Guber et al. / Environmental Modelling & Software 80 (2016) 185–200


