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INDIVIDUAL-BASED MODELING OF WHITE-TAILED DEER (*ODOCOILEUS VIRGINIANUS*) MOVEMENTS AND EPIZOOTIOLOGY

by

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B.S. University of Copenhagen, Denmark, 1998

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A Dissertation

Submitted in Partial Fulfillments of the Requirements for the

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DISSERTATION APPROVAL

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A Dissertation Submitted in Partial
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in the field of Zoology

Approved by:

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April 6, 2010

AN ABSTRACT OF THE DISSERTATION OF

LENE JUNG KJÆR, for the Doctor of Philosophy degree in ZOOLOGY, presented on April 6th, 2010, at Southern Illinois University Carbondale.

TITLE: Individual-based modeling of white-tailed deer (*Odocoileus virginianus*) movements and epizootiology

MAJOR PROFESSOR: Eric M. Schauber

White-tailed deer (*Odocoileus virginianus*) are important game mammals and potential reservoirs of diseases of domestic livestock, so diseases of deer are of great concern to wildlife managers. In many situations, models can be useful for integrating existing data, understanding disease transmission patterns, and predicting effects on host populations. Individual-based modeling (IBM) has become more commonplace in ecology as a tool to link individual behavior to population dynamics and community interactions, especially for gauging the effects of management actions. Spatially explicit IBMs are especially useful when ecological processes, such as disease transmission, are affected by the spatial composition of the environment.

I developed a spatially explicit IBM, DeerLandscapeDisease (DLD), to simulate direct and indirect disease transmission in white-tailed deer. Using data from GPS-collared deer in southern Illinois, I developed methods to identify habitats and times of high contact probability. I parameterized movement models, for use in DLD, using field data from GPS-collared deer in both southern and east-central Illinois. I then used DLD to simulate deer movements and epizootiology in two different landscapes: a predominantly agricultural landscape with fragmented forest patches in east-central Illinois and a landscape dominated by forest in southern Illinois. Behavioral and demographic parameters that could not be estimated from the field data were estimated using published literature of deer ecology. I assumed that bioavailability of infectious pathogens deposited in the environment decreased exponentially. Transmission probabilities were estimated by fitting to published trends in infection prevalence, assuming that infection probability during an encounter was equal for all age classes, so infection prevalence varied with sex- and age-specific behavior.

DLD simulations of chronic wasting disease epizootiology demonstrated significant effects of landscape structure, social behavior, and mode of transmission on prevalence, emphasizing the importance of spatial, temporal and behavioral heterogeneity in disease modeling. These results demonstrate the utility of IBMs in incorporating spatio-temporal variables as well as animal behavior when predicting and modeling disease spread.

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This PhD has been a challenge, both on a personal and a professional level. It has been a great learning experience, and I appreciate the things I have learned along the way as well as the friends I have made. Thank you all!

PREFACE

Infectious disease has only recently been accepted as a major factor that influences ecology and population dynamics of wildlife species (McCallum and Dobson 1995). Ecologists used to assume that well-adapted wildlife populations were not influenced or threatened by diseases (Jones 1982). However, the pioneering work of Anderson and May (Anderson and May 1978, Anderson and May 1979, May and Anderson 1979) has resulted in an increased interest in the impact of diseases on population dynamics (McCallum and Dobson 1995). Recently, laboratory and field experiments have proven that disease can regulate animal populations (Tompkins et al. 2001). Reduction of habitat, contact with domestic livestock, and movement of animals by humans over great distances have caused wildlife populations to be more susceptible to transmissible diseases (Jones 1982). Wildlife reservoirs of diseases can pose threats to domestic species and humans, so there is much political and economic pressure to minimize these threats. The importance of managing and understanding disease is evident, and models can be very useful for understanding and predicting disease spread and transmission patterns.

Mathematical models of epizootiology are based on factors affecting force of infection, which is the probability per unit time that a susceptible individual will become infected. Some models are based on the assumption of frequency-dependent transmission, in which force of infection is dependent on the proportion of infected hosts rather than the population density of infected hosts (May and Anderson 1979, O'Keefe 2005). This mode of transmission is proposed to be the case in sexually -transmitted and vector-borne diseases (May and Anderson 1979) as well as in animals that form social groups. In social groups, group composition and number of encounters among individuals may be more or less constant despite variations in population size (de Jong et al. 1995). Density-dependent transmission, in contrast, is based on the assumption that contact rate and force of infection increase with population density (Anderson and May 1979). Whereas frequency-dependent transmission typically results in unstable host-pathogen dynamics with either disease or host extinction (Getz and Pickering 1983), density-dependent transmission can result in a stable equilibrium or regular cycles between the host and its pathogen (Anderson and May 1978). Real patterns of disease transmission probably lie in between these 2 extremes of frequency- and density-dependent transmission (Antonovics et al. 1995, Ramsey et al. 2002), depending on the particular social structure and contact behavior of the host species.

The white-tailed deer (*Odocoileus virginianus*) exhibits both social grouping behavior and solitary life stages (Hiller 1996), which makes the species an interesting study animal in relation to disease transmission. Movement patterns and contact rates of deer vary during the year. Deer have home ranges that vary in size according to season, and form small matriarchal groups with related individuals such as siblings or offspring (Nixon et al. 1991). The grouping tends to be quite stable and the tendency to group seems to be stronger during the winter, especially in cold and snowy climates (Nixon et al. 1991). During and after parturition, pregnant does isolate themselves to rear their fawns and stay within a smaller area in their home range (Nixon 1992). This time of year is also a main period of dispersal, especially for yearling males (Nixon et al. 1994, McCoy et al. 2005). Increasing populations of white-tailed deer in most of the United States (Hiller 1996) probably lead to higher contact rates between the individual deer, potentially increasing disease transmission. Because deer are important game mammals and potential reservoirs of disease to domestic livestock and other cervids, control of disease in deer is of great concern to wildlife managers (Hiller 1996).

Chronic wasting disease (CWD), a disease that has emerged within the last 40-50 years, is of particular concern to wildlife managers.. CWD is the only transmissible spongiform encephalopathy (TSE) found in free living animals, occurring in wild deer (*Odocoileus* spp.), elk and red deer (*Cervus elaphus*) (Miller et al. 2000, Williams et al. 2002), and recently moose (*Alces alces*) (Colorado Division of Wildlife 2005). Transmissible spongiform encephalopathies are caused by an abnormal form of proteinaceous agents called prions that are devoid of nucleic acids, are proteinase-resistant, and seem to support their own amplification in the host by converting normal prions into the abnormal form (Prusiner 1998, Belay et al. 2004, Bollinger et al. 2004). CWD is characterized by behavioral changes and loss of body condition due to the accumulation of prion protein in brain tissue (Miller et al. 2000). An incubation period of $\geq$ 15 months precedes clinical signs (Williams et al. 2002, Belay et al. 2004), after which the affected animal rarely survives longer than a year (Gross and Miller 2001, Williams et al. 2002). For animals infected with CWD, there is no evidence of recovery or immunity and no treatment options (Williams et al. 2002). The prion causing CWD has been isolated from saliva, blood, urine, and feces (Mathiason et al. 2006, Haley et al. 2009) and can persist for years in the environment (Williams et al. 2002, Miller and Williams 2003, Mathiason et al. 2009), so both direct and indirect contact are likely to be important in the transmission of this disease. CWD has not yet been proven to be vertically transmitted in utero (Miller et al. 1998, Gross and Miller 2001, Williams et al.

2002). Prevalence of CWD seems to be higher in mature males, possibly because of increased exposure to potentially infected individuals during the rut (Farnsworth et al. 2005). Current management options where CWD is established are limited to culling animals showing clinical signs of CWD (targeted culling), population reduction (untargeted culling), and regulating or prohibiting supplementary feeding of cervids (Gross and Miller 2001). In some states, surveillance programs have been implemented, and translocation of both free-ranging and farmed deer and elk are restricted to reduce the chances of CWD establishment in new areas (Gross and Miller 2001).

Little is known about the dynamics of CWD in free-living cervid populations, and understanding the disease is of great importance. Gross and Miller (2001) developed an individual-based model (IBM) to simulate the possible dynamics of CWD in mule deer (*Odocoileus hemionus*) populations. The model failed to achieve steady state equilibrium between susceptible and infected individuals in the population, due to the assumption that the effective contact rate is constant and so transmission is frequency-dependent. This assumption may be incorrect. Although deer form social groups, group size and social structure respond to changes in density (Kie and Bowyer 1999) so contact rate may be density-dependent also. The feasibility of both direct and indirect transmission of the CWD prion protein suggests a combination of frequency-dependent and density-dependent transmission, which could result in a stable equilibrium or regular cycles between the host and its pathogen (Anderson and May 1978). Modeling of CWD might not be plausible using simple non-spatial mathematical models assuming either density-dependent or frequency-dependent transmission. These models do not include the spatial heterogeneity or stochastic demographic processes known to be important in disease transmission and establishment (Fa et al. 2001, Gudelj and White 2004, Drake 2005). Instead, using a bottom-up approach, such as a spatially explicit IBM incorporating demographic stochasticity, may shed light on the form of the transmission-population curve for either direct or indirect contact.

Models of CWD epizootiology should include habitat heterogeneity and its effect on contact rate, because deer occupy a variety of habitats of different composition and landscape structure can influence CWD prevalence (Farnsworth et al. 2005). Including habitat heterogeneity is facilitated by a spatially explicit modeling framework. Spatially explicit IBMs are advantageous because they reproduce the natural pattern of infected and uninfected individuals becoming spatio-temporally segregated (Fa et al. 2001, Gudelj and White 2004), can incorporate detailed spatio-temporal variables, and allow stochasticity in the behaviors and fates of individuals (Wilson 1998). Such stochasticity could result in extinction of disease or host populations on a local scale (Beissinger 2000, Drake 2005). Fa et al. (2001) developed an IBM of rabbit viral hemorrhagic disease based on transmission through direct contact, and found transmission to be density-dependent. Smith et al. (2001) developed an IBM to investigate the effectiveness of measures to control bovine tuberculosis in the European badger (*Meles meles*). Their results propose a different control measure than simple mathematical models, thus demonstrating that incorporation of spatio-temporal variables can greatly affect model outcome and identify more effective disease control strategies. IBMs are thought to be especially useful when investigating the effects of population sex and age structure, spatial structure of the environment, and individual variation on disease dynamics (Conner et al. 2007).

The objectives for my research were to 1) Quantify white-tailed deer movement patterns and contact rates and 2) use those results to create an agent-based spatially explicit model that simulates the spread of chronic wasting disease within white-tailed deer populations. Chapter 1 provides a method for measuring contact habitat using data from GPS collared deer and has been published as Kjær et al. (2008). Chapter 2 reports analyses of individual deer movement as well as movement within deer groups, based on data from GPS-collared deer. Chapter 3 describes the IBM, DeerLandscapeDisease (DLD) and provides results from scenarios where I investigate the effect of landscape and mode of transmission on the transmission and prevalence of CWD.

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CHAPTER 1: SPATIAL AND TEMPORAL ANALYSIS OF CONTACT RATES IN FEMALE WHITE-TAILED DEER

INTRODUCTION

Wildlife diseases are gathering increasing attention due to their impact on livestock, humans, and endangered or threatened species (McCallum and Dobson 1995, Daszak 2000, Chomel et al. 2007). Reduction of habitat, contact with domestic livestock, toxicant exposure, and transport of animals by humans over great distances have altered the susceptibility and exposure of wildlife populations to diseases (Galloway and Handy 2003, Fisk et al. 2005, Chomel et al. 2007). Because wildlife diseases can threaten domestic animals and humans, stakeholders exert political and economical pressure to actively manage wildlife disease via both lethal and nonlethal approaches (Peterson et al. 2006).

Ecological factors can affect disease dynamics in wild populations by influencing rates and patterns of transmission. Therefore, information about ecological factors affecting transmission will enable managers to more effectively reduce threats posed by wildlife diseases. Pathogens can transmit by either direct contact, which requires animals to be close in time and space, or indirect contact, where only spatial proximity is required. For example, rabies transmits directly through saliva (Sterner and Smith 2006), whereas chronic wasting disease (CWD) transmits through both direct and indirect contacts because the etiologic agent can persist in the environment (Williams et al. 2002, Miller and Wild 2004, Miller et al. 2004, Miller et al. 2006)

Contact rates among free-ranging animals can be affected by social grouping, concentrated resources (Miller et al. 2003, Gompper and Wright 2005, Wright and

Gompper 2005), landscape structure (Fa et al. 2001, Gudelj and White 2004), and population density (de Jong et al. 1995, Ramsey et al. 2002). In social species where group composition is stable, the likelihood of an infected host contacting, and therefore infecting, members of the same group is higher than for non-members (Altizer et al. 2003, Schauber et al. 2007). By definition, animals interact with members of the same group both more often and more intimately than with individuals from other groups. However, a pathogen must ultimately be transmitted to other groups to persist. The fluid group structure in white-tailed deer (*Odocoileus virginianus*) may increase intergroup contact rates and, potentially, disease transmission (Hawkins and Klimstra 1970, Nixon et al. 1994, Comer et al. 2005). Hawkins and Klimstra (1970) reported that separate social groups of white-tailed deer often fed together in later winter and spring but rarely bedded together. Congregation of multiple groups at feeding sites therefore could accelerate contact rates. Aggregation of Rocky Mountain elk (*Cervus elaphus)* at artificial feedings sites in Wyoming facilitates transmission of brucellosis (*Brucella abortus;* (Dobson and Meagher 1996, Cross et al. 2007). Transmission of bovine tuberculosis (*Mycobacterium bovis*) in white-tailed deer is also facilitated by congregation at feeding sites (Miller et al. 2003, Palmer et al. 2004). Land use and land cover affect deer behavior and movement across the landscape, and therefore affect contact rates. Farnsworth et al. (2005) found that CWD prevalence in mule deer (*O. hemionus*) was higher in developed areas than in undeveloped areas, suggesting higher contact rates on developed land. Deer activity patterns and social cohesion also vary temporally, which could produce predictable changes in contact rates. The effects of moon phase on deer activity and movement are ambiguous. Some studies have not found any influence of moon phase on deer activity

(Zagata and Haugen 1974, Kufeld et al. 1988, Beier and McCullough 1990), whereas others have reported that deer movements increased during a full moon (Kammermeyer 1975 cited in Beier and McCullough 1990) and use of open habitats decreased during a full moon (Beier and McCullough 1990). Finally, deer are crepuscular, so elevated contact rates at dawn and dusk would indicate that contacts occur mainly when deer are moving, whereas elevated contacts during midday would indicate that contacts occur mainly while bedding.

Understanding factors that mediate contact rates could aid in managing or predicting the spread and persistence of diseases in deer, and I found no studies in the literature that analyze temporal and spatial influences on contact rates in deer. New technologies, such as remote cameras (Beringer et al. 2004), contact loggers (Ji et al. 2005), and Global Positioning System (GPS) collars (Schauber et al. 2007) facilitate the study of contacts between individual animals. My objectives were to test whether certain landcover types serve as foci for intergroup contacts between deer using GPS collar locations and to determine if seasonal and daily variations in behavior affect contact probabilities.

STUDY AREA

I conducted my study in an exurban setting approximately 4 km southeast of Carbondale, Illinois, USA (37° 42´14´´N, 89° 9´2´´E). The climate was characterized by moderate winters and hot, humid summers, with a mean January low temperature of -6.2° C and mean July high temperature of 31° C (Midwestern Regional Climate Center 2007). The study area comprised a mix of contiguous patches of oak-hickory forest (57%) with some hay fields and other grasslands (26%). Row crop agriculture (12%) consisted primarily of soybeans, and the area had minor components of urban land use including lawns and old fields. Average fixed-kernel home range sizes for female deer in the study area were 53.0 ± 5.2 ha during the fawning season and 90.6 ± 9.7 ha during the winter season (Storm et al. 2007). The study area and exurban Carbondale deer population are further described elsewhere (Schauber et al. 2007, Storm et al. 2007).

METHODS

Deer Capture and Handling

I captured deer at sites baited with corn or apples, primarily by darting with 3-cc barbed darts (Pneu-Dart, Inc., Williamsport, PA) containing 2:1 mix of Telazol HCL (4 mg/kg; Fort Dodge Animal Health, Fort Dodge, IA) and xylazine HCL (2 mg/kg; Bayer Corp., Shawnee Mission, KS; Kilpatrick and Spohr 1999). I fired darts from elevated stands approximately 20 m away from the bait site, and each dart contained a radiotransmitter for locating darted animals. I also used rocket-propelled nets (Hawkins et al. 1968) or drop nets (Ramsey 1968) to capture deer, which I then immobilized with an intramuscular injection of 10 mg/kg ketamine HCL (Fort Dodge Animal Health, Fort Dodge, IA). I blindfolded all deer during handling and visually observed them after handling until they were able to stand on their own. I specifically focused on capturing females >1 year old. Although I captured and collared some fawns and males, I programmed their collars to drop off (see below) after only a few months to avoid constriction due to growth in fawns and neck swelling of bucks during the rut. I did not include males in analyses due to small sample size. Deer capture and handling methods were approved by the Southern Illinois University Carbondale Institutional Animal Care and Use Committee (protocol no. 03-003).

I fitted 27 female deer with GPS collars (Model TGW-3500, wt 700 g; Telonics, Mesa, AZ), that stored location data internally with a manufacturer-reported error range of 13-36 m. Schauber et al. (2007) found median and 95th percentile position errors were 8.8 m and 30 m, respectively, for stationary collars under closed canopy. Collars deployed in 2002 and 2003 recorded locations hourly and I programmed their release mechanisms to drop off after 4-5.5 months. I programmed collars deployed in 2004-2005 to record deer locations every 2 hours and to drop off after 12-17 months. However, collars recorded locations every hour in November and December to account for greater deer activity during the rut. I programmed all collars to determine locations within 3 minutes of one another, and I excluded estimated locations with elevation >100 m different from the known elevation of the study area. I also excluded locations from the first 3 days after capture to account for altered behavior due to capture and handling. I identified 3 pairs of deer as being in the same social groups because their movements were highly correlated (Schauber et al. 2007), and my analysis only included pairs of deer in different groups. To account for seasonal variations in behavior, I separated location data into 4 seasons pertinent to deer biology: gestation (1 Jan - 14 May), fawning (15 May - 31 Aug), prerut (1 Sep - 31 Oct), and rut (1 Nov - 31 Dec).

My sampling unit for all contact analyses was a pair of deer. I defined 2 deer to be in direct contact if their concurrent GPS locations were <25 m apart. I chose this proximity criterion as the median of the GPS-collar accuracy. I calculated the location of each direct contact between 2 deer as the midpoint between their concurrent GPS locations (Schauber et al. 2007).

Spatial and Temporal Analysis of Contact Rates

I used ArcView 3.2 to create a digital map of the landcover types (Table 1) in a 10 ×10-km area encompassing all known locations of the GPS-collared deer. I used 1998 digital orthophoto quarter quadrangles (Illinois Geospatial Data Clearing House (IGDCH) 1997) and ground-truthing to identify and delineate landcover types (Storm et al. 2007).

I used compositional analysis (Aebischer and Robertson 1992, Aebischer et al. 1993) to compare landcover types where 2 deer came in contact with landcover types jointly used by the 2 deer. Using the digital map of the study area, I characterized the landcover associated with each contact by calculating the proportion of each cover type (Table 1) within a 12.5-m radius buffer (to account for GPS errors) centered on the contact location. I averaged these proportions over all contact locations for a given deer pair and season to represent used landcover. To reduce problems associated with zero use values (Bingham and Brennan 2004), I excluded from analysis for each season any landcover type that was unused (seasonal use value = 0) by $\geq$80% of deer pairs in that season.

I used the joint utilization distribution (JUD) of a deer pair in a given season to define available landcover for contacts. The JUD describes the joint probability that both members of a pair will be found in the same area, assuming independent movements. The JUD thus indicates both the amount of space jointly used and how similarly the 2 animals use space within that overlap zone (Millspaugh et al. 2004). I used JUD to define available landcover, first because 2 deer are unlikely to contact each other outside both animals' home ranges or in areas of exclusive use. Second, and perhaps more importantly, deer clearly select particular habitats (e.g., ecotones) within their home ranges; such selection is well-documented and thus not especially interesting for my analyses. Simply put, little would be learned if I determined that deer are most likely to contact other deer in preferred deer habitat. Therefore, I specifically sought to test whether deer contacts occur in certain habitats more frequently than would be expected on the basis of their joint use. Because the JUD indicates the probability the 2 deer will be located concurrently in the same area assuming independent movements, a difference in landcover proportions between contact locations and JUD essentially indicates that the direct contact rate (i.e., proportion of concurrent locations in a given landcover type that are <25 m apart) differs among land cover types. In other words, does the tendency of 2 deer to approach one another in a particular area, given that they both use that area, differ depending on the area's landcover type? To calculate the JUD, I first estimated the fixed-kernel utilization distribution (Seaman and Powell 1996, Seaman et al. 1998) from 200 randomly selected GPS locations for each deer and season, with smoothing parameter estimated by least-squares cross validation in the Home Range extension (Rodgers et al. 2005) in ArcView 3.2:

$$\mathrm{UD}(i,s)_{\mathrm{xy}} = \frac{\sum_{k=1}^{200} \exp\left[-\frac{(x-x_k)^2+(y-y_k)^2}{2h^2}\right]}{200\times 2\pi h^2}$$

where x and y are coordinates on the landscape, x_k and y_k are coordinates of location k within the set of 200 locations for deer i and season s, and h is the smoothing parameter.

The denominator adjusts for sample size and ensures that the UD has volume = 1. I used 200 locations per home range to balance sample size requirements for fixed-kernel home ranges while minimizing computing time (Seaman et al. 1999).

I then calculated the seasonal JUD of each deer pair (*i* and *j*) as the product of the 2 utilization distributions at each point in a grid with 40-m spacing overlaying the study area: $\text{JUD}(ij,s)_{xy} = \text{UD}(i,s)_{xy} \times \text{UD}(j,s)_{xy}$. I chose 40-m spacing to ensure thorough coverage ($\geq$500 points within a typical home range; Storm et al. 2007) while reducing computation time. Note that neither UD nor JUD is a discrete area; both take nonzero (albeit often extremely small) values for any coordinates within or beyond the study area. Unlike the UD, the JUD has volume <1. The JUD also differs from the volume of intersection (Millspaugh et al. 2004) in accounting for home range size; 2 deer with perfectly overlapping home ranges will have volume of intersection = 1 no matter their home range size. However, large home ranges dilute the opportunity for simultaneous occupancy at a given location, which is reflected in low JUD.

I calculated available landcover proportions for each deer pair as the weighted average (wt = JUD) proportions of the landcover types within the JUD:

$$\hat{p}_a = \frac{\sum_{cell=1}^{N} p_{a,cell} \overline{\text{JUD}}_{cell}}{\sum_{cell=1}^{N} \overline{\text{JUD}}_{cell}}$$

where $\hat{p}_a$ is the weighted average proportion of landcover type a, $p_{a,cell}$ is the proportion of landcover type a in a given cell, $\overline{\text{JUD}}_{cell}$ is the average JUD value of the cell's 4 corners, and N is the number of cells in the study area. Recall that the JUD is not a discrete area, but landcover types in areas with infrequent joint use by a deer pair were given low weight. Weighting by JUD gave small available proportions for some landcover types and deer pairs. The smallest available proportion associated with a nonzero use proportion was 10^{-9}, so I treated every landcover type with available proportion below 10^{-10} (one order of magnitude smaller; Aebischer et al. 1993) as unavailable (zero availability) to remove small values. If a particular landcover type was unavailable to a deer pair, I treated it as a missing value. As indicated previously, I excluded landcover types in each season with zero use by ≥80% of deer pairs. Because compositional analysis is based on log ratios and log(0) is undefined, I replaced zero use proportions with values of 10^{-10} for available landcover types included in the analysis.

In the compositional analysis, the resulting log-ratios were not normally distributed, so I used randomization to test the global null hypothesis of random distribution of contacts with respect to joint use ($\alpha = 0.05$ throughout) and to test for pairwise differences in contact frequencies among cover types. I used the BYCOMP macro (Ott and Hovey 2002) in SAS (SAS Institute, Cary, NC) to perform compositional analysis. Because all tests were based on 999 randomizations of the data, the smallest obtainable *P*-value was 0.001.

I calculated average number of contacts per deer pair per season. I used mixed-model logistic regression (SAS PROC GLIMMIX) to test how contact rates varied among seasons (as described in GPS Collar Data), lunar phases (quarters of the lunar cycle centered on the new, full, waning, and quarter moons), and diel periods (dawn: 0300-0900 hr, midday: 0900-1500 hr, dusk: 1500-2100 hr, and night: 2100-0300 hr). The binary response variable was whether each pair of concurrent locations for a deer pair were ≤25 m apart. I treated deer pair as a random effect and temporal variables as fixed effects. I initially fitted a model with all possible interactions among fixed effects but then dropped the nonsignificant 3-way interaction and any nonsignificant 2-way interactions. I used Tukey's multiple range test to separate means.

RESULTS

Spatial and Temporal Analysis

Compared with joint space use (JUD), contacts did not occur randomly among landcover types during gestation, fawning, and rut seasons (all $P \leq 0.023$, Table 2), whereas I did not find that contacts in prerut ($n = 15$ pairs) differed from random use ($P = 0.1$, Table 2). The following results are all based on differences in logratios of used habitat versus available habitat. During gestation ($n = 23$ pairs), contact rates were higher in forest than in any other cover. Road cover had lower contact rates than lawn and grassland (Figure 1a). During the fawning season ($n = 13$ pairs), contact rates were higher in agricultural fields and grassland than in road and lawn cover and also higher in agricultural fields than in forest (Figure 1). Contact rates during the rut ($n = 23$ pairs) were higher in forest than grassland, water, agricultural fields, and lawn (Figure 1). Average number of contacts per deer pair were 19.67 (SE = 5.30), 8.86 (SE = 3.32), 6.17 (SE = 2.15), and 16.07 (SE = 6.98) for the gestation, fawning, prerut, and rut seasons, respectively. The effect of diel period on contact rates varied with season ($F_{9,838} = 4.90$, $P < 0.001$), with contact rates high at night and low around dawn during fawning and high at dusk and low at dawn during prerut, rut, and gestation (Figure 2a). In general, there was an > 2-fold difference in contact rates between rut and fawning season with rut having the highest contact rates (Figure 2a). Contact rates also differed among lunar phases ($F_{3,838} = 9.14$, $P < 0.001$), being approximately 30% higher during full moon than in other seasons (Figure 2b).

DISCUSSION

Because I used JUDs to assess available landcover types, differences I found in contact rate among landcover types are not simply due to differences in the amount of time deer spend in such landcover. Instead, my findings reflect differences in behavior of deer while they occupy different landcover types. My results indicate that contact is more likely in habitats where deer feed or take cover, corresponding to what is known about seasonal activity patterns and habitat selection of deer. Deer tend to aggregate in areas with high food availability (Miller et al. 2003, Gompper and Wright 2005, Wright and Gompper 2005) such as growing agricultural crops (Nixon et al. 1991, Vercauteren and Hygnstrom 1998). High contact probabilities in agricultural fields during the fawning season could be explained by the crops planted in my study area (corn and soybeans) mainly growing during late spring and summer. The high contact probabilities in forest during the rut and gestation seasons (fall-winter) could also reflect use of forest habitat as concealment and thermal cover.

Contact rates between females were elevated during the rut, a time of high activity by deer of both sexes, particularly during midday, perhaps because females are more active during the day in fall (Beier and McCullough 1990). As expected, contact probabilities were high during gestation, when deer tend to form larger groups (Hawkins and Klimstra 1970, Nixon et al. 1991) and low during fawning season when female deer isolate themselves (Bertrand et al. 1996). Decreased contact probabilities during midday in the fawning season may reflect deer being able to meet their nutritional needs in a shorter time on summer forage and therefore avoiding activity in midday heat (Beier and McCullough 1990). Elevated contact rates during full moon could reflect increased nocturnal activity, but the observed lunar effect was generally slight.

My novel application of compositional analysis to test for habitat-specific contact rates presents both advantages and challenges. Despite some complex mathematics for calculating UDs and JUDs, my approach can easily be used whenever concurrent animal locations and landcover data are available. Designating as used the landcover types around contact locations for a pair of deer is straightforward, but the designation of available landcover is challenging. The JUD provides a pre-existing metric of habitat-specific joint use, and using JUD to define available landcover types allows researchers to disentangle behaviors specifically related to contact (i.e., approach vs. avoidance upon detection) from individual habitat utilization and space use in the absence of animals from other social groups. Some drawbacks of applying compositional analysis to study contact patterns are 0% use values and small availability values for some landcover types, both of which present problems associated with log transformation. I minimized these problems by excluding rarely used landcover types and determining the replacement value for zeroes by the smallest value for used landcover.

Instead of JUDs, I could have defined available habitat on the basis of the combined utilization distribution of each pair (summing the UDs to indicate probability of either animal using the area but not necessarily both), but doing so would prevent me from interpreting the results in the context of contact rates. An even simpler approach would be to delineate a discrete area of joint use for each pair of animals, which would avoid excessively small availability values. However, discrete home range overlap provides no measure of space use within the overlap zone and thus cannot delineate if contacts occurs in a specific habitat because of specific deer behavior or because of higher levels of space use by both animals.

In analyzing temporal patterns of contact rates, I used mixed-model analysis to account for non-independence of the set of concurrent locations from each pair of animals. A simpler approach would have been to calculate the contact rate in each season as a proportion (one data point per pair per season, perhaps arcsine-transformed) and analyze with a standard repeated-measures approach. However, arcsine transformation does not account for variance in proportions associated with the number of trials (i.e., concurrent locations), which are likely to differ among pairs and seasons. Besides accounting for differing numbers of trials, the mixed-model approach can also account for missing data because all pairs may not be monitored in all temporal periods.

I only analyzed collared female deer due to neck swelling in bucks during the rut. Monitoring bucks would offer insights into intersexual contacts and potential for sexual transmission of pathogens. Sexual contact may be a transmission route of CWD, because CWD prevalence is elevated in mature bucks (Farnsworth et al. 2005). The use of expandable collars to monitor intra- and intersexual contacts involving bucks should be considered for further studies of disease transmission in deer.

My identification of contacts is limited by the accuracy of the GPS collars I used. Collar accuracy could affect my contact estimates and my proximity criterion of 25 m could cause an overestimation of direct contact rate. However, Schauber et al. (2007) found that location errors caused observed distances between GPS collars to generally exceed the true distance, indicating that my criterion of 25 m may actually underestimate the true contact rate. Also, the likelihood of effective contact (i.e., contact sufficient for disease transmission) given that 2 deer in different groups come within 25 m of each other is unknown. However, I assume that probability of effective contact is a positive function of the probability of 1 deer coming within 25 m of another deer.

The use of bait sites for deer capture could impact local contact rates, providing concentrated food resources during the capture season. Kilpatrick and Stober (2002) noticed that deer shifted their core areas to encompass a bait site within their home ranges. Most of my bait sites were located in grassland cover, which could have caused elevated contact frequencies in this landcover type. I used bait from October to March, which covers prerut to gestation. In the compositional analysis I did find grassland to have a high ranking for prerut, rut, and gestation, but I also observed the same pattern for the fawning season when no bait sites were present. I know of one private landowner in my study site who baited deer on his property year round, but none of my contacts were situated near that bait site. Therefore, I did not find clear evidence that bait sites substantially affected landcover-specific contact rates, but nevertheless the potential effect of bait sites on contact rates should not be discounted.

MANAGEMENT IMPLICATIONS

My research provides wildlife managers with information about effects of landscape composition, season, and diel period on contact rates in deer. Knowledge of how such factors affect contact rates could help wildlife managers in projecting the effects of habitat alteration on disease transmission, as well as identifying variables that need to be investigated in future field research, such as relative frequency of contact during feeding, bedding, and traveling. Furthermore, my methods can aid in targeting areas for population management to potentially reduce contacts and disease spread. My finding of elevated female-female contact rates during rut indicates that management practices affecting breeding behavior, e.g., immunocontraception, can affect both intra- and intersexual contact.

CHAPTER 2: MODELING WHITE-TAILED DEER MOVEMENT FROM GPS LOCATION DATA FOR USE IN AN INDIVIDUAL-BASED MODEL

INTRODUCTION

Individual-based modeling (IBM) is a promising tool for modeling spatially explicit population processes, particularly regarding the transmission of wildlife diseases. Spatially explicit IBMs are advantageous because they can incorporate detailed spatio-temporal variables as well as stochasticity in the behaviors and fates of individuals (Wilson 1998). Stochastic processes can potentially lead to infected and uninfected individuals being spatio-temporally segregated (Fa et al. 2001, Gudelj and White 2004). Such stochasticity could result in extinction of disease or host populations on a local scale (Beissinger 2000, Drake 2005).

Movement is an essential component of an IBM but can be very difficult to model (Topping et al. 2003). The most common movement models (e.g. simple, correlated, and biased random walks) are vector-based and depend on step lengths and turn angles (Turchin 1998). An animal might stay in a certain movement behavior, such as dispersal, foraging or bedding, for a specific amount of time but may change that behavior depending on habitat or behavioral state (Morales et al. 2004, Gurarie et al. 2009). For example, animals dispersing or moving in suboptimal habitat may move in relatively straight lines (turn angle close to 0) with longer distances between stops, whereas movement within a home range or in good foraging habitat may be more tortuous with smaller distances between stops and larger turning angles (Morales et al. 2004).

Animals use different habitats for different purposes such as bedding, foraging, hiding, or dispersing..White-tailed deer feed in forest, grassland and agricultural crops

(Nixon et al. 1991, Vercauteren and Hygnstrom 1998). During the winter deer typically bed down in closed forest during the evening and night, but bed down in fields exposed to the sun during the day (Armstrong et al. 1983). Rohm et al. (2007) found that fawns were typically hidden along grassland-forest edges in southern Illinois. Long et al. (2005) have shown that deer dispersal rate, average dispersal distance, and maximum dispersal distance can be affected by the amount and composition of forest cover in the landscape. Habitat use and the tendency of the white-tailed deer to form social groups both change over the course of a year (Hawkins and Klimstra 1970, Nixon et al. 1994, Comer et al. 2005), making the species an interesting study animal in relation to both individual and group movement.

Various IBMs have been developed relating individual and group movements to landscape features (Morales et al. 2004, Forester et al. 2007, Aarts et al. 2008, Gurarie et al. 2009), with most of them being some variation of correlated random walks (CRWs). Such IBMs can also incorporate within-group behaviors, as with the IBM created by Puga-Gonzalez et al. (2009) to simulate macaque (*Macaca spp.*) group formation and social interactions based on dominance/submissive behavior. In their IBM, simulating group foraging in sheep, Dumont and Hill (2001) based the grouping behavior on an attraction variable that could be varied depending on the individual state of the sheep. Eftimie et al.(2007) used attraction and repulsion variables when modeling group formation in a general grouping model.

When no physical observation of animals and their movements are available, methods that rely on Global Positioning System (GPS)-collar locations may be advantageous. I here present novel movement analysis methods previously only used on elk (*Cervus elaphus*), using GPS-collar locations of white-tailed deer.. Furthermore I present a simple way to model group movement, also based solely on GPS-collar locations. These methods will provide me with models for both individual movement and group movement of deer, to be used in an IBM for disease transmission in deer populations.. Following Morales et al. (2004), I used a Bayesian framework to model individual movement with ≥ 1 movement model, then modeled group movement to match the observed distribution of distance between group members.

METHODS

Study Area

I conducted my study from 2006-2008 at 2 different study sites: an exurban setting approximately 4 km southeast of Carbondale, southern Illinois, USA (37° 42´14´´N, 89° 9´2´´E) from 2002-2006 and an agricultural setting around Lake Shelbyville, east-central Illinois, USA (39° 24' 30" N, 88° 46 '40" W). The climate at the southern Illinois study site was characterized by moderate winters and hot, humid summers, with a mean January low temperature of -6.2° C and mean July high temperature of 31° C (Midwestern Regional Climate Center 2009). At the east-central Illinois study site, winters were slightly colder with hot, humid summers. Mean January low temperature was -9.4° C and mean July high temperature was 31° C (Midwest Regional Climate Center 2009). The southern Illinois area comprised a mix of contiguous patches of oak-hickory forest (57%) with some hay fields and other grasslands (26%). Row crop agriculture (12%) consisted primarily of soybeans. The east-central Illinois study site consisted mainly of agricultural fields (70%, soybeans and corn) with 13% oak-hickory forest mainly situated around the lake itself. Both study sites had minor components of water and urban land use including lawns and old fields. Average fixed-kernel home range sizes for female deer in the southern Illinois study area were 53.0 ± 5.2 ha during the fawning season and 90.6 ± 9.7 ha during the winter season (Storm et al. 2007). At the east-central Illinois study area, average home range size was 47.8 ± 3.9 ha during the winter and 22.5 ± 2.0 ha during the fawning season (Kjær et al., unpublished data). The landscape and deer population in the southern Illinois study area are further described elsewhere (Schauber et al. 2007, Storm et al. 2007, Kjær et al. 2008).

Deer Capture and Handling

At both study sites, white-tailed deer were captured at baited sites by darting, rocket-propelled nets, drop nets (Rongstad and McCabe 1984), and Clover traps (Clover 1956). The darts were fired from elevated stands ca. 20 m away from bait site, and darts contained a radio transmitter for locating darted animals. The darts contained 2:1 mix of Telazol HCL and Xylazine HCL (Kilpatrick and Spohr 1999). Net-captured deer were immobilized with an intramuscular injection of ketamine HCL (10 mg/kg) and xylazine HCL (2 mg/kg) (Kilpatrick and Spohr 1999). During the winters of 2002-2006, I caught a total of 46 deer at the southern Illinois study site and fitted 30 deer with GPS collars (Model TGW-3500, wt 700 g; Telonics, Mesa, AZ). During the winters of 2006-2009 I caught a total of 122 deer and fitted 22 deer with GPS collars (Model TGW-3500, wt 700 g; Telonics, Mesa, AZ) at the east-central Illinois study site. All deer were blindfolded during handling and visually observed after handling until they were able to stand on their own. Deer capture and handling methods were approved by the Southern Illinois University Southern Illinois Institutional Animal Care and Use Committee (protocols no. 03-003 and 06-002).

For movement analysis, I used location data from GPS collars deployed on 52 deer (Table 3). The GPS collars stored location data internally with a manufacturer-reported error range of 13-36 m. Schauber et al. (2007) found median and 95th percentile position errors were 8.8 m and 30 m, respectively, for stationary collars under closed canopy. Collars deployed in 2002 and 2003 recorded locations hourly and I programmed their release mechanisms to drop off after 4-5.5 months. I programmed collars deployed in 2004-2005 and in 2006-2008 to record deer locations every 2 hours and to drop off after 12-17 months. However, collars recorded locations every hour in November and December to account for greater deer activity during the rut. I programmed all collars to determine locations within 3 minutes of one another, and I excluded estimated locations with elevation >100 m different from the known elevation of the study areas. I also excluded locations from the first 3 days after capture to account for altered behavior due to capture and handling. I identified 2 pairs of deer at the southern Illinois study site and 2 pairs of deer at the east-central Illinois study site as being in the same social groups because their movements were highly correlated (Schauber et al., 2007). To account for seasonal variations in behavior, I separated location data into 4 seasons pertinent to deer biology: gestation (1 Jan - 14 May), fawning (15 May - 31 Aug), prerut (1 Sep - 31 Oct), and rut (1 Nov - 31 Dec).

Spatial and Temporal Analysis of Movement

Using ArcMap 9.2 (ESRI, 1999-2006), I created a digital map of the landcover types in a 10 ×10-km area of the southern Illinois study site and a 30 × 130-km area of the east-central Illinois study site encompassing all known locations of the GPS-collared deer. I used 1997 and 2003 digital orthophoto quarter quadrangles (Illinois Geospatial Data Clearing House (IGDCH) 1997, 2003) and ground-truthing to identify and delineate landcover types (Storm et al. 2007) (Table 4). I plotted the individual locations from the 30 and 22 GPS–collared deer in the southern Illinois and Shelbyville landscape maps (respectively) in ArcMap 9.2 and used Hawth's tools (Beyer 2004) to calculate step lengths and turn angles. I also calculated distance from each location to all possible cover types using the Spatial Analyst extension

Individual Movement Models

Using methods as in Morales et al. (2004), I represented deer movement by fitting ≥ 1 random walks (RW) to the GPS movement data, consisting of pairs of bi-hourly and hourly (dependent on season) step lengths (r_t) and turning angles (θ_t). Movement patterns were assumed to depend on the behavioral state of the animal, and the fitting procedure assigned each observation to one in a number of movement states to find the distributions of step lengths and turn angles for each behavioral state that best fit the the data. Each observation was assumed to be independently drawn from a Weibull distribution (for step length) and a wrapped Cauchy (for turn angle). I chose the Weibull distribution for step lengths because it can mimic a number of statistical distributions, such as the normal and exponential distribution (Morales et al. 2004). The probability density function for the Weibull distribution takes the following form:

$$f(\underline{r}) = abr^{b-1}\exp(-ar^{b}) \tag{1}$$

with a as the scale parameter and b as the shape parameter (Morales et al. 2004). The wrapped Cauchy distribution is commonly used for modeling circular data. The probability density function for the wrapped Cauchy distribution takes the form:

$$f(\theta) = \frac{1}{2\pi} \times \frac{1-\rho^2}{1+\rho^2 - 2\rho\cos(\theta-\mu)} \quad 0 \le \theta \le 2\pi, \quad 0 \le \rho \le 1 \tag{2}$$

where θ is the turn angle, μ is the mean turn angle, and ρ is the mean cosine of the angular distribution, which controls the spread of the distribution (Morales et al. 2004).

Different models can be fitted to data by incorporating different numbers of random walks with fixed probabilities for switching between behavioral states, or with switching probabilities being dependent on landscape features. I did not observe dispersal of our study animals in either study site, although a few animals exhibited exploratory movement behavior in which they would leave their home range for ca. 1 day to then return to the home range. Because this exploratory behavior was infrequent and not all animals in my study sites exhibited this behavior, I did not try to include it in my models. Whereas Morales et al. (2004) had up to 3 different behavioral states, I choose to only model at most 2 behavioral states – fast and slow movement. These states could possibly represent feeding and/or bedding and movement between feeding and bedding areas.

I parameterized the following 5 models from Morales et al. (2004):

1) Single: a single RW was fitted to data

2) Double: a mixture of 2 RWs with no model for switching. Each observation (at time t) was assigned a probability (η_{1t}) of being in movement state 1 (η_{2t} = 1- η_{1t}).

3) Double switch: 2 RWs with fixed switching probabilities. I used a 2×2 matrix that defined the probabilities q_{ijt} of being in movement state i (= 1 or 2) at time t+1 given that the individual was in state j (= 1 or 2) at time t.

4) Double with covariates: 2 RWs with the probability of being in movement state i related to habitat of current location (h_t out of H possible habitat types, Table 4) via a logit link:

$$\eta_{1t} = \exp(v_h)/(1+\exp(v_h)), \quad h=1,\ldots,H \tag{3}$$

$$\eta_{2t} = 1 - \eta_{1t}$$

5) Double switch with covariates: Same as in 3) but with the probability of switching from fast to slow movement being a function of distance to habitat types.

$$\begin{aligned} q_{21} &= \exp\left(\beta_1 + \sum_{h=1}^{H} m_h d_h\right) \Big/ \left(1 + \exp\left(\beta_1 + \sum_{h=1}^{H} m_h d_h\right)\right) \\ q_{11} &= 1 - q_{21} \end{aligned} \tag{4}$$

with parameters β_1 and m_h where d_h is distance (km) to habitat h. The thought behind this model was that deer may be more likely to switch from fast to slow movementwhen they are close to optimal foraging habitat

All models were fitted using Markov-Chain Monte-Carlo (MCMC) in Winbugs 1.4.3. (Bayesian Analysis Using Gibbs Sampler; (Lunn et al. 2000, Spiegelhalter et al. 2003), freely available at http://www.mrc-bsu.cam.ac.uk/bugs/). I ran 3 MCMC chains for each model with 20,000 iterations for each chain. I examined autocorrelations and convergence to stationary distributions in sample paths of the parameters. Convergence is reached when the quantiles of interest for the posterior distributions do not depend on the starting points of the MCMC simulations. For each chain, the first 5000 iterations were discarded to eliminate initial fluctuations and, to avoid auto-correlation, I only kept every 10th MCMC sample for posterior estimation. This gave me a total of 3×1500 independent MCMC observations from which to estimate the posterior distribution of each parameter. I used vague priors (Table 5) for each of my models.

To compare the performance of different models, I used the Deviance Information Criterion (*DIC*) (Spiegelhalter et al. 2002), a Bayesian generalization of Akaike's Information Criterion (AIC) that is given by

$$DIC = Dev(\bar{\theta}) + p_D \tag{5}$$

Model complexity is measured by the “effective number of parameters”, $p_{D,}$ and similar to Spiegelhalter et al. (1998) and Gelman et al. (2004), I estimated p_D by:

$$p_D = Var\,(Dev)/2 \tag{6}$$

Models with smaller DIC are better supported by the data. I also analyzed the ability of the models to reproduce observed properties of the data by examining whether autocorrelation functions (acf) of simulated movement paths were similar to those observed in the data (Morales et al. 2004). For each model I sampled from the posterior distributions of parameters using 5000 replicates and then simulated a movement path. The acf of the bi-hourly or hourly distance moved was then graphically compared to the observed acf.

Group Movement

I quantified correlation of movements to identify pairs of female deer in a group together in each study site (Schauber et al. 2007). For each such within-group pair, I calculated the distance between simultaneous locations at each time (x_t). Because I only had 2 deer pairs per study site, the distance data for both study sites were pooled. I then fitted exponential distributions ($f(x) = \lambda\exp(-\lambda x)$) to seasonal within-group distances using EasyFit 5.2 Professional (MathWave Technologies, Dnepropetrovsk, Ukraine), to estimate λ values for each season.

RESULTS

For the Single model, convergence of the Markov chains was usually reached within the first 5000 iterations. For the more complex models, a substantial proportion of deer data sets failed to converge even after 80,000 iterations, so the sample sizes (numbers of individual deer yielding usable results) for these more complex models were considerably smaller than for the Single model. The Single model was the most parsimonious model for both landscapes, all deer, and for all 4 seasons (Appendix A).). The rank order of performance of the other 4 models varied among individuals. The more complex models did not provide a closer match of the observed acfs of movement paths, further supporting selection of the Single model based on DIC values (Figure 3). Turn angle distributions did not show a particular pattern across seasons or study sites (Figure 4 and 5) but were generally broad and not centered on zero, indicating that movement paths were quite tortuous. Step lengths were generally larger in the east-central Illinois study site than the southern Illinois study site (Figure 6 and 7), and modal step lengths were similar to the distance across deer home ranges. Appendix B shows the means of the posterior distribution of model parameters for all 5 models. Distances between group members were greatest in fawning and prerut seasons (Figure 8), and mean distances from the fitted exponential distributions were 226 m for gestation, 302 m for fawning, 315 m for prerut and 246 m for rut seasons.

DISCUSSION

Using a Bayesian approach allowed me to fit different movement models to the data, although the a model incorporating only one behavioral state provided the most parsimonious fit for the movement data. Furthermore, fitting exponential distributions to group movement data revealed a seasonal difference in distance data, caused by differences in deer seasonal behavior.

Several models on animal movements have shown that habitat can affect the movement of animals... Webb et al. (2009) found indications that female white-tailed deer moved more tortuously within than outside of foraging patches. Similarly, Jiang et al. (2009) found a positive relationship between tortuousity and the number of bedding sites and feeding sites in an area, and a negative relationship between tortuousity and the total basal area of tree stems in their study of roe deer (*Capreolus capreolus*) movement. I was not able to distinguish between habitat-specific movement patterns, nor aswas I able to distinguish between behavioral states in my analysis of individual movement, as a model comprising only 1 random walk was most supported. Morales et al. (2004) found that the more complex models such as the double switch, the double with covariates, and the switch with covariates better fitted their elk (*Cervus elaphus*) data. The reason for these models better describing their data could be the difference in time scale between my study and that of Morales et al. (2004). Whereas they analyzed distance moved per day, I analyzed distance moved per 1-2 hours. The elk from the Morales et al. (2004) study were translocated at the start of their study and so their elk were still dispersing and potentially establishing home ranges. The deer in my study site moved within established home ranges, so the time scale I used may have been too coarse to detect differences in movement related to different behavioral states such as bedding and feeding. Furthermore, the turn angles from my analysis were not generally centered on zero as would be expected from correlated random walks. This indicates a lot of reversals of the deer and could be a result of home range behavior and movement. With modal step lengths similar to home range diameters, reversals would be expected as the animals restrict their movement to be within their home range. The fact that the steps I analyzed generally carried the animal across its home range supports the conclusion that the time scale used in my analysis may be too coarse when analyzing within-home range movement.

My results suggest that when detailing movement in well-established populations with minimal dispersal, the time scale of the data collected is of great importance. Webb et al. (2009) used GPS collars recording data every 15 minutes and Jiang et al. (2009) looked at deer tracks and trails to obtain data for analysis. These data represent much finer time scales than my data. These fine time scales may be more appropriate when trying to distinguish between different movement states or when relating movement to the habitat of the moving animal. However, the inability of my models to improve my representation of movement relative to the Single model may not be a disadvantage –

complex is not always better, especially in modeling processes that operate on long time frames (e.g., disease transmission). A simple movement model may be an advantage for an IBM, where computing time is a limiting factor. Furthermore, in an IBM, methods and agents behaviors are updated at certain time steps throughout the model run time. If these time steps are set to hours instead of minutes, modeling more complex movement behavior may not be relevant, and the Single model may be a better option. However, the Single model may not be able to reflect movements such as dispersal and exploratory excursions, and these types of movement should be modeled separately.

I found that step lengths were longer in the east-central Illinois study site than the southern Illinois study site .This could reflect an effect of habitat on deer movement, since the east-central Illinois study site has more fragmented forest patches than the southern Illinois study site. Movement within a home range may be governed by the spatial distribution of resources, quality of the habitat (Webb et al. 2009) or cover (Beier and McCullough 1990) and the fragmented forest landscape in our east-central Illinois study site could cause deer to move with longer step lengths through sub-optimal habitat, such as habitats with patchy resources or less cover. The movement analysis of Webb et al. (2009) showed more tortous movement of white-tailed deer in foraging patches, suggesting more straight line movement between such patches. The analysis of Jiang et al. (2009) also found roe deer movement paths to be more tortuous in areas with numerous bedding and feeding sites, further suggesting slower movement in areas with cover or resources. The predominantly agricultural landscape of east-central Illinois may have provided patchy cover and resources causing average step lengths to be larger between these patches.

Group members tended to be further apart during the fawning season. This was to be expected because my group distances were calculated from female-female pairs, and the fawning season is when matriarchal groups dissolve and does isolate themselves to rear their fawns (Nixon 1992, Bertrand et al. 1996). In an Ohio study, Sorensen and Taylor (1995) found that group sizes of female white-tailed deer increased from fall (October/November) to winter (December – February), and in southern Illinois, Hawkins and Klimstra (1970) found that doe groups on average regrouped around October after the fawning season group break-ups. These findings could explain the longer distances between group members during the prerut season, seeing that females are still rearing their fawns and just starting to group up with other individuals.

In Puga-Gonzalez et al.'s (2009) IBM on macaque behavior, grouping behavior was determined by decisions of aggression or submission, which produced similar affiliation patterns as those observed from empirical data. The IBM of Dumont and Hill (2001) modeled grouping behavior as an attraction parameter depending on the behavioral state of the animal, and found that simulation results were consistent with field data. Both these models were based on and validated against detailed available empirical data namely physical observations. I did not have the opportunity to physically observe deer grouping behavior for prolonged periods of time during my study, mainly due to logistical restrictions and accessibility to the study areas. When physical observations of the study animals are not feasible, finding other means of estimating animal behavior becomes important. The use of GPS data in my study provided me with an extensive data set, from which IIwas able to use simple methods to quantify grouping movement.

The IBMs of Puga-Gonzales et al. (2009) and Dumont and Hill (2001), were solely created to model grouping behavior. In IBMs where the grouping behavior is not the main purpose, but merely a part of the agent behavior within the model, simpler ways of modeling grouping behavior might be preferable in terms of computing time and extent of coding. My group analysis method is relatively simple and the results can easily be fitted into an IBM incorporating group movement with little extra coding. Given the simplicity of my method, it can be extended to other social species, provided enough GPS data are available to determine group membership and that the sample size of group distances is large enough for distribution fitting.

CAVEATS

The accuracy of the GPS collars I used might have affected the calculated group distances. Schauber et al. (2007) found that location errors caused observed distances between nearby GPS collars to generally exceed the true distance, so my calculated distances between group members may be greater than the true distances. More detailed information on male movement behavior would be of great value when creating models simulating deer behavior and movement, since I would expect male movement to be different from female movement as a result of differences in behavior. The larger home ranges of male white-tailed deer (Hawkins and Klimstra 1970, Marchinton and Hirth 1984, Webb et al. 2009) and increased activity levels during the rut, with bucks chasing females and movement over large distances (Marchinton and Hirth 1984) would cause male movement patterns to be different than those of females.

CHAPTER 3: DEERLANDSCAPEDISEASE: A SPATIALLY EXPLICIT INDIVIDUAL-BASED MODEL, SIMULATING DISEASE TRANSMISSION IN WHITE-TAILED DEER

INTRODUCTION

Wildlife epizootics are challenging to eradicate or control. Transmission of wildlife diseases to livestock or humans emphasizes the importance of managing and understanding disease. Epizootiological models can be very useful for understanding and predicting disease spread and transmission patterns. Classical mathematical models assume that force of infection is dependent on either the proportion of infected hosts (frequency dependent transmission) or the population density of infected hosts (density dependent transmission) (May and Anderson 1979, O'Keefe 2005), yet many diseases may not follow this strict pattern of transmission. In addition, the transmission and establishment of disease within a population are highly stochastic processes affected by both habitat heterogeneity and demographics (Fa et al. 2001, Gudelj and White 2004, Drake 2005). A diseased animal might become spatially isolated or surrounded by other infected animals, thus reducing the transmission of disease to conspecifics. An animal may die before it can transmit the disease, extinguishing an epizootic before it can begin. Spatially explicit individual-based models (IBMs) are advantageous because they can reproduce stochastic spatio-temporal segregation of infected and uninfected individuals (Fa et al. 2001, Gudelj and White 2004), and can incorporate detailed spatio-temporal variables, individual variations, and demographic stochasticity (Wilson 1998, Conner et al. 2007).

Several IBMs have been used in the field of epizootiology, such as models of rabbit viral hemorrhagic disease (Fa et al. 2001) and bovine tuberculosis in badgers (Smith et al. 2001). However, these models incorporate only direct contact as a transmission pathway and do not incorporate empirically-based movement behaviors. Bovine tuberculosis may be spread through both direct and indirect contact (Palmer and Whipple 2006), and other diseases such as chronic wasting disease also show evidence of both direct and indirect transmission (Williams et al. 2002). Furthermore, disease transmission is dependent on contact rates that in turn are determined by how animals move within their environment (indirect contact) and in relation to other animals (direct contact). The effect of animal movement on contact rates and thus disease transmission indicates that incorporating realistic movement behaviors into models of disease transmission may be of great importance.

I developed DeerLandscapeDisease (DLD), a spatially explicit individual-based model (IBM) to simulate ecological and behavioral factors affecting disease transmission and persistence in white-tailed deer and predict prevalence levels resulting from these factors. DLD was created to incorporate different landscapes, and the model can easily import any raster layers or GIS projections of interest to the modeler. The animal model specifically simulates behavior of white-tailed deer thought to influence population dynamics and disease transmission, such as movement, mating and grouping behavior. The disease component in DLD allows for pathogen build-up in the environment, and contacts between individual deer, either direct or indirect, are modeled as a stochastic process depending on movement of the animals involved.

I here use DLD to simulate transmission of chronic wasting disease (CWD) in white-tailed deer. CWD is the only transmissible spongiform encephalopathy (TSE) found in free-ranging wildlife (Williams et al. 2002). Affected species are deer, elk (Miller et al. 2000, Williams et al. 2002) and recently moose (Colorado Division of Wildlife 2005). CWD affects the central nervous tissue and is characterized by behavioral changes, such as excessive salivation, tremors, lack of coordination, difficulty swallowing, increased drinking and urination and loss of body condition and ultimately death (Miller et al. 2000). The CWD prion has been found in saliva, blood, urine, and feces (Mathiason et al. 2006, Haley et al. 2009) and can remain infective in the environment for years (Williams et al. 2002, Miller and Williams 2003, Mathiason et al. 2009), so both direct and indirect transmission of CWD may occur. However, little is known about the strength of each infection route and the subsequent effect of CWD on population densities within wild animal populations. CWD has not yet been proven to be vertically transmitted (Miller et al. 1998, Gross and Miller 2001, Williams et al. 2002).

I use published data on CWD and empirical data on deer behavior to create scenarios of CWD transmission and run scenarios for both direct and indirect transmission of the disease. I use the model to assess the effects of landscape and transmission mode on prevalence and population impacts. I also simulate the potential effects of deer removal by reducing deer group size, as this reduction in deer group size may simulate lower deer densities.

METHODS

Model Construction

DLD was created using the Repast Simphony platform (North et al. 2005, North et al. 2007) and Java programming language (Sun Microsystems, Oracle Corporation, RedWood City, CA). I chose Repast Simphony over platforms such as SWARM (Minar et al. 1996), NETLOGO (Wilensky 1999) and MASON (Luke et al. 2004) due to its user friendly graphical user interface, its ability to incorporate raster files and shape files, and the ability to run from standalone batch files. Furthermore, Repast Simphony is free and open-source.

Landscape Description

The two different landscapes I use in the model are based on sites of multi-year field studies in southern Illinois and east-central Illinois described in chapter 2. For each study site I created a 10x10 km raster map of landcover with a pixel size of 25x25 m. I used 1997 and 2003 digital orthophoto quarter quadrangles (Illinois Geospatial Data Clearing House (IGDCH) 1997, 2003) and ground-truthing to identify and delineate landcover types (Table 6). The raster maps (Figure 9) were then imported into Repast Simphony (North et al. 2005, North et al. 2007). I will refer to the southern Illinois landscape as the contiguous forest landscape, and the east-central Illinois landscape as the fragmented forest landscape. I used periodic boundaries (Topping et al. 2003) in my model landscapes.

Animal Model

I used the results of analyzing movement data from GPS-collared deer (Chapter 2) to develop my animal model. 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 3 different agents: adult females, adult males and fawns. Each time step in the model was 2 hours, the same time interval as the locations provided by most of my GPS collars.

Movement. Each adult deer in the model creates a home range that is based on maximum and minimum home range sizes (Table 7) and on cover type percentages from field data. Home range centers of different individuals can not occupy the same pixel unless the individuals are related. If the animal is not able to establish a home range according to 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.

Individual movement is modeled as correlated random walks, with various combinations of step lengths and turn angles depending on the state of the animal (Morales et al. 2004). Using methods similar to Morales et al. (2004), I fitted Weibull distributions to my step length data and wrapped Cauchy distributions to my turn angles. For my movement model fitting I allowed for up to two behavioral states (fast and slow movement) but a single behavioral state was the most parsimonious representation for both the contiguous forest landscape and the fragmented forest landscape (Chapter 2). Dispersal, exploratory movement and mating movement were modeled separately with different turn angle distributions (Table 8).

Movement in the model also implements a Gaussian probability for turning towards the home range center the further the distance away:

$$P = 1 - e^{-((\Delta x^2/2\sigma_x^2))+(\Delta y^2/2\sigma_y^2))}$$

where Δx and Δy are the 2 spatial dimensions of the displacement of the current location from the home range center, σ_x and σ_y control home range size in the x and y dimensions.

White-tailed deer form groups during most of the year. Males form loose bachelor groups except during the rut (Hirth 1977, Halls 1984, Marchinton 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 1992).

To model group movement, 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 drawn from a seasonal-specific exponential distribution (Table 8). Females only form groups with related individuals (i.e. offspring, mothers, siblings). However, because I start out with no fawns at time zero in the model, females are allowed to group with unrelated individuals until their first fawns turned into adults. I added this feature to simulate "normal" group and behavior dynamics from time 0. If an agent leaves a group (Table 7), 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).

The first two months of a fawn’s life are mostly spent hiding and bedding down, waiting for the mother doe (Marchinton and Hirth 1984), so I 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 (see under fawn maturation). To ensure that fawn and mother stay close, distance vectors were drawn from an exponential distribution with a mean $\lambda = 0.1$ m until the fawn is 6 months old (Table 8). After that the fawn will use the same distance distribution as for general group movement. If the mother of a fawn older than 2 months dies the fawn will inherit the home range of its mother and move as in individual movement (see earlier). In the model fawns will not join the dead mother’s group although this has been observed in nature (Woodson et al. 1980). From personal observations during my field studies, adult does would show aggressive behavior toward non-offspring to allow their own fawns to get to the food source. This behavior can counter-argue the joining of groups by orphaned fawns. The model can be easily modified to have the fawn join its mothers group if the mother dies. 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 (Table 7). These percentages lie within values reported for yearling dispersal for both agricultural and forested landscapes (Hawkins et al. 1971, Nixon et al. 1994, Rosenberry et al. 1999, Nixon et al. 2007). Most of the GPS-collared deer in my field study exhibited exploratory movements, usually during gestation and rut (Kjaer et al. 2009, unpublished data) and usually lasting <1 day (Schauber et al. 2007). Based on the observed frequency of excursions from my field data, I calculated an average chance of exploratory behavior for each individual deer to be 2% (over the entire season) for both gestation and rut and used this value in the model (Table 7). Both dispersal and exploratory movement are modeled with the same step lengths as normal movement but with a turn angle distribution concentrated around zero (Table 8) producing more linear paths. 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.

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 the maximum home range radius found in the actual landscapes). 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 (Marchinton and Hirth 1984). Because males are known to follow potential mates at close distances during the rut (Halls 1984, Marchinton 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. Once mated, a doe gives birth 187-222 days (randomly chosen) later (Marchinton and Hirth 1984) to 1 (0.25 probability), 2 (0.5), or 3 (0.25) fawns. 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. 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. I used yearly mortality rates of 0.4 for males and 0.2 for females (Table 7). These values lie within reported values for both agricultural landscapes (Nixon et al. 1991, Nixon et al. 1994) and more forested landscapes (Hawkins et al. 1970, Nixon et al. 1994). I used annual mortality of 0.44 for fawns <2 months of age and 0.2 for fawns >2 months (Table 7). 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 (Marchinton and Hirth 1984), so I assumed that an older fawn could survive the death of its mother but a fawn <2 months old in the model died if the mother died.

Disease. I assumed 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. These functions are modeled using a Gaussian cumulative distribution function (cdf) with μ = 20 months (latent period of 18 months + 2 months) and σ = 4 months, so the diseased deer nears maximum infectivity at 30 months post-infection, which is also the time where death due to disease approaches 100%. I 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 (Williams et al. 2002, Belay et al. 2004). 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. This way the animal will not have an increased mortality rate during the latent period, but mortality approaches 100% by 30 months since infection.

Prions are persistent in the environment for at least several years (Williams et al. 2002). To model this, I assumed that the pool of available, infective pathogens declines exponentially after deposition in the environment with a half life of 6 months. 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.

The probability of infection given direct or indirect contact is unknown. I adjusted the probability of infection given contact so that prevalence in the model corresponds with CWD prevalence in Wisconsin's endemic southwest core area (Wisconsin Department of Natural Resources 2009a). There, the highest prevalence was found in males and they reported an average rise in prevalence from 0.1 in 2002 to ca. 0.15 in 2008 (Wisconsin Department of Natural Resources 2009a). Matching this rise in prevalence in the fragmented forest landscape yielded a chance of infection of 0.0128 for direct contacts and 1.2×10^{-5} for indirect contacts (here the value is lower, due to prion accumulation in the landscape). The same probabilities of infection given contact were used for the contiguous forest landscape to allow direct assessment of the effect of landscape structure. I 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.

Scenarios

I created 6 different scenarios to investigate the importance of landscape structure, mode of transmission, and group size on disease spread and host population dynamics. I ran direct and indirect transmission scenarios for both the fragmented forest landscape and the contiguous forest landscape (4 scenarios). I explored the efficacy of general (e.g., increased public harvest) as opposed to localized culling (e.g., sharpshooting entire groups) in the fragmented forest landscape by reducing maximum group sizes to half of the default values (female group size: 2, male group size: 5) at the same overall population size. I only reduced group sizes given direct transmission, because I expected the effect of reduced groups to be higher for direct contacts (Schauber et al. 2007). Six hundred replicates of each scenario were run for 20 simulation years. Starting population of animals comprised 400 male and 400 female deer, with a CWD prevalence of 0.1. Temporal patterns of prevalence (arcsine square root transformed) were compared among scenarios using repeated measures profile analysis in SAS 9.2 (SAS Institute, Cary, NC). The same analysis was used to compare prevalence between males, females, and fawns within scenarios. I also compared prevalence between young (≤ 3 years) and old (> 3 years) males and females to examine how prevalence changes with age. When comparing age and sex groups, I omitted year 1 and 2 in the repeated measurements profile analysis to avoid missing values for old males and females in those years. To investigate whether differences between observed prevalence patterns in my model and prevalence found in field studies could be attributed to difficulties in detecting early disease infection, I re-analyzed my data using only animals infected for at least 6 months using same methods as above. I also calculated the annual force of infection (ζ) for each scenario as the proportion of susceptible animals at year t that had become infected by year $t + 1$. To assess whether transmission in my model corresponded better to density-dependent or frequency-dependent concepts, I correlated ζ at time t against infectious (infected >6 months) prevalence at time t (frequency dependence), and the density of either infected or infectious animals (infected >6 months) at time t (density dependence). CWD in DLD is modeled as having a latent period, so I only used prevalence and densities of animals infected > 6 months, since animals at an advanced disease stage have a larger impact on disease transmission. To account for delays in prion accumulation in the indirect-transmission scenarios, I also correlated force of infection at time t against the above mentioned variables at time t-1 and time t-2.

RESULTS

Without the disease component, populations grew at an average rate of 2.25% per year and population sizes after 20 years averaged ca.1500 animals for both landscapes (Figure 10). Adding the disease component to the model caused population decline in most of the fragmented forest scenarios, which had an average yearly decline of 1.61% for direct transmission runs and 5.08% for indirect transmission runs (Figure 10). Population size for the direct scenario with reduced group size stayed fairly constant throughout the 20 years with an average decline of 1.2% per year. For the contiguous forest landscape, populations increased by 0.04%/yr for direct transmission with default groups, 0.64%/yr for direct transmission with reduced group size scenarios, and 0.36% for indirect transmission scenarios (Figure 10).

Not surprisingly, given the large number of replicated simulations, all repeated measures analyses of total and infectious prevalence indicated significant scenario*time and age/sex category*time interactions (all $F_{68,11693} > 10$, $P < 0.0001$). For both direct and indirect transmission, prevalence was higher in the fragmented forest landscape than the contiguous forest landscape (Figure 11A). Indirect transmission resulted in higher prevalence than did direct transmission scenarios in the fragmented landscape, and scenarios with reduced group sizes had lower prevalence than both direct with regular group sizes and indirect scenarios (Figure 11A). Prevalence levels for indirect transmission in the fragmented landscape started to decrease around year 13 (Figure 11A) although population size for this scenario started to decrease around year 4. With direct transmission in the fragmented forest landscape, prevalence decreased after year 4, although population sizes remained fairly constant around 800 individuals (Figure 10). The contiguous forest landscape showed little difference between default and reduced group sizes (Figure 11A), although prevalence decreased after year 4 with no subsequent decrease in population size (Figure 11A). In the contiguous forest landscape, prevalence levels for indirect transmission were initially lower than for direct contact, but started to increase around year 12 and ended up having higher prevalence than the direct scenarios (Figure 11A). Infectious prevalence (deer infected >6 months) levels were lower, but differences among scenarios were qualitatively similar as for total prevalence (Figure 11B).

With direct transmission, prevalence was higher in males, whereas prevalence values in fawns, females and old females were similar (Figure 12A-B, Figure 14A-B). When only including animals infected longer than 6 months, the difference between age and sex groups in the direct scenarios was mainly due to higher prevalence in males and lower prevalence in fawns (Figure 13A-B, Figure 15A-B). Prevalence in old males was higher than in young males for all direct scenarios. For the indirect scenarios the differences in prevalence levels were mainly due to lower prevalence in fawns (Figures 12C, 13C, 14C, 15C).

Force of infection varied over the years for all scenarios and showed the same trends in variation as the prevalence for all scenarios (Figure 16). For the direct scenarios, force of infection was highest during the first years of the simulation runs. Maximum values were 6.5% in year 3 for the fragmented forest landscape with a yearly average of 3.9%, 4.5% in year 2 for the contiguous forest landscape with a yearly average of 1.6%. Maximum force of infection was 5.5% in year 3 for the fragmented forest landscape with reduced group size with a yearly average of 3.3%, and 3.9% in year 2 for the contiguous forest landscape with reduced group size with a yearly average of 1.3%. For the indirect scenarios, the contiguous forest landscape had a maximum force of infection rate of 2.4% in year 2 with a yearly average of 1.1%, whereas the maximum value was 7.3% at year 11 for the fragmented forest landscape with a yearly average of 5.6% (Figure 16). Correlation analysis suggested that the density of either infected or infectious animals (infected >6 months) was a better predictor of force of infection (Table 9). For all the indirect transmission scenarios, the correlation coefficients were higher when force of infection at time t was analyzed against all variables at time t-2 (Table 9).

DISCUSSION

DLD allowed me to explore the profound effects of both habitat heterogeneity and mode of transmission on disease transmission and subsequent prevalence in white-tailed deer. Prevalence levels were higher in the fragmented forest landscape and were generally higher for indirect transmission scenarios. In addition, my model results suggested that population-level impacts of CWD may differ substantially depending on landscape structure. Finally, my bottom-up simulation of movements resulted in force of infection that was more strongly related to density than prevalence of infectious animals.

Disease in the fragmented landscape had a negative impact on population growth to the point where the deer population was decreasing. In the contiguous forest landscape this impact was slighter and I still saw population growth albeit smaller than in scenarios without the disease component. These population impacts can be explained by differences in prevalence between the two landscapes, and this in turn can be explained by agent behavior within the model. White-tailed deer need a component of forest cover within their home range (Marchinton and Hirth 1984), so a landscape with fragmented forest patches tends to concentrate deer more in those patches thus increasing the local density and hence the potential for both direct and indirect contacts. Farnsworth et al. (2005) found that human land use could affect CWD prevalence in mule deer, where destruction of suitable habitat due to development might cause a concentration of mule deer in suitable fragmented patches, increasing local population density and thus accelerating transmission of CWD. As simulated population sizes decreased in DLD, I found that prevalence in the fragmented forest landscape decreased concomitantly when transmission was direct, and the host-disease system approached a stable equilibrium.

With indirect transmission, I observed a time-delay from when population size decreased to the resultant decrease in prevalence. This delayed response when the disease is transmitted indirectly occurs because the disease can continue to be transmitted even after the death of the diseased individual due to prion accumulation in the environment. The longer pathogens remain infective and available in the environment, the greater they can accumulate and the more pronounced the time delay. Prevalence levels in the contiguous forest landscape still decreased within the direct transmission scenario even though I observed an increase in population size. This could be due to low local densities resulting from animals being more spatially dispersed in the forest landscape. Although prevalence levels in the indirect transmission scenarios were lower than in the direct, I do see an indication of these prevalence levels increasing by the end of the scenario runs.

The higher prevalence in male deer, especially older males, is also observed in empirical studies of CWD, potentially due to differences in behavior or physiology (Farnsworth et al. 2005, Miller and Conner 2005, Grear et al. 2006, Osnas et al. 2009, Wisconsin Department of Natural Resources 2009a). In my model, males are part of larger groups and move around more than females, leaving and joining new groups. Furthermore, I model males to follow females around during the rut, which could potentially add to infection exposure. Female behavior within my model does not seem to increase the risk of infection with time, since I do not see an increase in prevalence for old females.

For my model runs with direct transmission, infection prevalence was very similar in fawns and adult females when I included all infected animals. In empirical studies, however, observed CWD prevalence is generally lower in fawns than adults

(Grear et al. 2006, Wisconsin Department of Natural Resources 2009a). This discrepancy could be explained by difficulties in detecting early stage infection with standard diagnostic tests (Haley et al. 2009, Mathiason et al. 2009). Mathiason et al. (2009) found that the time from environmental exposure to first detection of the CWD prion using tonsillar biopsies in white-tailed deer varied from 6 to 18 months and the authors suggest using blood-based testing to detect pre-clinical CWD infection. My results when including only animals infected longer than 6 months mirror the lower apparent prevalence in fawns compared to all other age classes. I also observed lower prevalence in fawns than in adults in the scenarios with indirect transmission. These results can be explained by transmission not being a result of contact between individuals but being a question of time of exposure to the pathogen. Fawns would have had less time to be exposed to prions in the environment.

CWD can be transmitted through both direct animal contact and environmental sources (Miller and Williams 2003, Williams and Miller 2003, Mathiason et al. 2006, Haley et al. 2009, Mathiason et al. 2009), but the strength of each pathway and how much they each contribute to the transmission and persistence of CWD in free-living populations are unknown. I chose to separate the different modes of transmission in my model runs, to investigate possible effects on model outcome. The difference in prevalence that I found may be explained by direct transmission being more stochastic, insofar that the contacts are very time-dependent and there is a higher chance of disease extinction, due to death of diseased animals. Indirect transmission can continue even after the death of the diseased individual, due to accumulation of persistent pathogens (e.g., prions) in the environment, so disease transmission is more reliably dependent on duration of exposure. Also, Schauber et al.(2007) found that indirect contact rates among female deer were much less strongly influenced by social group membership than were direct contact rates, with indirect contacts being driven mainly by the amount of shared space. Although indirect transmission is dependent on how animals move and overlap in habitat and space use, it does not require simultaneous space use, which could explain why prevalence was similar across adult sex and age classes in the indirect scenarios.

Transmission of disease within social groups has often been used as a justification to assume frequency-dependent transmission, as group composition and number of encounters between or among individuals may be more or less constant despite variations in population size (May and Anderson 1979, O'Keefe 2005). However, some species may exhibit more flexible group structures with varying group sizes, and this pattern is especially seen in white-tailed deer male bachelor groups (Hirth 1977, Halls 1984, Marchinton and Hirth 1984, Nixon et al. 1994). My results showed that reduction of deer group sizes affected prevalence levels in the direct transmission scenarios for both landscapes, although the difference in the contiguous landscape was small due to low prevalence levels. This reduction of group sizes in the model reduced the transmission potential within groups and thus affected disease transmission between groups as well. I explored these scenarios to compare increased hunting pressure or unselective culling (which would increase mortality generally) with strategies where entire groups are culled (which would reduce the number of groups, but not group size). Both selective and non-selective culling have been the preferred means of CWD management in free-ranging populations (Williams and Miller 2002, Wasserberg et al. 2009). Uncertainties about mode of transmission can hinder choosing management strategies for disease eradication

(Wasserberg et al. 2009). Assuming direct transmission, culling and reduction of populations could result in population thresholds below which the disease is not able to persist in the population (Anderson and May 1978). Using a multi-state computer simulation model, Wasserberg et al. (2009) found that hunted deer populations exhibited lower CWD prevalence than non-hunted populations, suggesting that population density and turnover affect CWD transmission and that culling may be a suitable strategy for CWD management. Lower population densities might reduce joint space use and chance of indirect contacts. However the potential for re-colonization and subsequent reemergence of the disease caused by environmental contaminants poses a challenge to disease management, and further research is needed to expand our understanding of environmental prion accumulation as a route of disease transmission.

The force of infection measures the rate of disease spread within a population, and my results varied between landscapes and transmission modes. Within a landscape, indirect transmission seemed to produce a higher force of infection than direct transmission. Prevalence levels in the contiguous forest landscape were still very low, but appeared to be increasing in the last years of simulation runs. If run for longer than 20 years, I would expect the force of infection to increase as prevalence increases. The force of infection was slightly better predicted by density than prevalence of infected animals (infected >6 months). These results suggest that disease transmission of CWD within my model may resemble density-dependent transmission or may be an intermediate of density- and frequency-dependent transmission. Both density-dependent transmission and an intermediate of density- and frequency-dependent transmission within my model could potentially result in co-existence of CWD and deer, but the lack of long term empirical data prevents me from validating my findings.

For indirect transmission with persistent pathogens, I found that the force of infection was better predicted by the density of infected animals present 2 years earlier. This time delay can be explained by indirect transmission not being an instantaneous process, but that there is a time delay between an animal depositing the prion in the environment, and the subsequent transfer to susceptible animals as well as the time it takes for prions to accumulate in the environment. To my knowledge, no estimates of force of infection estimates of CWD have been published in scientific journals, however the Wisconsin Department of Natural Resources (Wisconsin Department of Natural Resources 2009b) have preliminary results from a study conducted in the western core of their CWD endemic areas. Although force of infection values varied across years, they report an average yearly increase in the force of infection rate of 4%, suggesting an increase over time in the rates of CWD transmission across the area. For my direct scenarios force of infection decreased over time as the numbers of susceptible host were decreasing. Even in the contiguous landscapes where population numbers were still increasing, I observed a decrease in the force of infection over the simulation years. Only the indirect transmission scenarios showed an increase in the force of infection, but only during parts of the simulation runs. The discrepancy between my model results and the Wisconsin study suggests that more studies are needed to estimate force of infection rates in CWD endemic areas and if possible relate them to population density and prevalence rates to determine transmission patterns of CWD

CWD has only recently been discovered in wildlife populations and is of great concern to wildlife managers and public alike. The need to understand and predict CWD dynamics is evident and developing models to make predictions and pinpoint areas of interest in CWD research could be of great value. Gross and Miller (2001) developed a mechanistic IBM, simulating CWD transmission in mule deer populations. Their model failed to predict long-term co-existence of disease and deer populations, their model lacked spatial components and assumed fixed contact rates. DLD incorporates spatial- and temporal stochasticity and imposes no top-down assumptions regarding contact rates – in this model contact rates, both indirect and direct, are emergent properties of the movement behavior of agents within the model. Gross and Miller (2001) acknowledge that the limited amount of data from long-term surveillance can complicate making long-term predictions. Because of this limitation I chose to run DLD for a maximum of 20 years, since further predictions would need to be validated by field studies. Although CWD reduced deer density within my model, the effect of CWD on wild deer populations is still unknown for some areas with CWD. However, in areas where CWD has been occurring for a prolonged time period, evidence exists that CWD does affect population dynamics of wild cervids. In northern Colorado, Miller et al. (2008) found prevalence levels in mule deer ranging from 20-40% in a population that had been declining over the last 20 years, and this decline coincided with the emergences of CWD in the population. As with any model, caution must be taken not to rely too heavily on projected scenarios. Many aspects of CWD dynamics are still unknown and I strongly support further surveillance of CWD and research into the underlying factors promoting prion transmission. More extensive research into infectivity and environmental pathways is needed to improve on predictive modeling.

DLD provides an excellent tool for investigating how different disease transmission pathways can affect prevalence levels within a population. My results indicate that indirect transmission poses a greater challenge to disease eradication or control. Indirect transmission is a more consistent transmission pathway than the highly stochastic direct pathway and the potential for pathogen accumulation causes higher and less variable prevalence levels. Furthermore prevalence levels in the model are less affected by behavioral differences between the sexes and age groups, as well as current population density, when the transmission is indirect than when it is direct. However, conclusion is tentative, as some age- and sex-specific behaviors (e.g., scraping and other marking behaviors, or fighting) were not included in the model. Although targeting certain age or sex groups through culling may prevent a disease from spreading to neighboring populations through dispersal (Oyer et al. 2007, Skuldt et al. 2009), selective culling may not have as big an effect to eradicate or control an already established disease in a population if that disease is being transmitted through indirect contact. The complications of eradicating a pathogen in the environment pose a further challenge when trying to manage an indirectly transmitted disease (Williams and Miller 2000, Williams et al. 2002, Miller et al. 2004).

DLD is adaptable to simulate most diseases in deer. Disease parameters can be altered to fit the disease under investigation, and landscapes can be imported to fit the desired habitat of interest. DLD is still being developed and fine tuned but the aim is to make the model available to researchers and wildlife managers through the Cooperative Wildlife Research Laboratory's home page in the near future.

CAVEATS

I did not include density-dependence in survival and recruitment rates in the model, but density dependence could prevent or reduce decreases in population size due to disease (Gross and Miller 2001). Density-dependence could be incorporated into later versions of DLD. I did not include the potential for infected carcasses to stay in the landscape and add to environmental contamination (Williams and Miller 2002, Miller et al. 2004) nor did I add scraping sites of bucks that may also serve as a potential hot spot for indirect disease transmission (Alexy et al. 2001). Furthermore, I did not remove home range fidelity at end stages of the disease to simulate behavioral anomalies caused by CWD (Williams and Miller 2000, Miller and Wild 2004). These are aspects that might have an effect on transmission levels and may be incorporated in later versions of DLD.

Table 1. Landcover types used in analyzing contact habitat for white-tailed deer in southern Illinois, 2002-06. Percentages can be obtained by dividing total areas by 100.

Landcover code	Total area (ha)	Description of cover type
agriculture	1405.6	Agricultural fields, mainly corn and soybeans
aqua[a]	7.5	Aquaculture center
fish[a]	16.0	Fish hatchery
forest	5565.2	Forest consisting mainly of oak-hickory
grassland	609.9	Native grasses, not mowed
lawn	427.9	Mowed and tended lawns close to buildings
marsh[a]	13.9	Marsh
oldfield	136.7	Field in late successional state, with brush and trees
pasture	442.6	Grassy fields, grazed by livestock
road	80.0	Highways, roads and gravel roads
urban	117.7	Buildings and houses
water	1181.2	Lakes, ponds, and rivers

[a] No home ranges overlapped these cover types, and they were omitted from all analyses.

Table 2. Seasonal tests for random distribution of pairwise contact locations among landcover types for between-group pairs of female white-tailed deer in southern Illinois, 2002-06.

Season	Wilk's Lambda	*F*	df	*P*
gestation	0.37	4.91	6,17	0.004
fawning	0.23	7.59	4,9	0.002
prerut	0.60	2.64	3,12	0.100
rut	0.57	3.64	4,19	0.023

Table 3. Location data from GPS collars deployed on white-tailed deer captured in the southern Illinois study area, 2002-2006 and the east-central Illinois study area, winter 2006-2009. F = female, M = male, A = adult, Y = yearling, F = fawn.

Study site	Eartag #	Sex	Age	# of locations	Capture date	End date
southern Illinois						
	1	F	Y	10,491	12/06/2004	03/01/2006
	2	F	A	2,816	12/06/2003	05/10/2004
	3	F	A	2,659	11/08/2003	02/02/2005
	4	F	Y	2,494	10/06/2003	03/15/2004
	5	M	Y	233	11/08/2002	11/22/2002
	6	F	A	3,809	02/13/2003	08/01/2003
	7	M	A	3,693	02/18/2003	08/01/2003
	8	F	F	3,404	02/24/2003	08/01/2003
	9	M	F	3,416	02/24/2003	08/01/2003
	10	F	F	4,048	09/25/2003	03/15/2004
	11	F	A	3,773	11/08/2004	11/18/2005
	12	F	A	3,725	11/17/2004	03/01/2006
	13	F	A	7,598	10/30/2002	02/26/2003
	14	F	A	3,680	11/03/2004	03/01/2006
	15	F	Y	3,639	10/25/2004	03/01/2006
	16	F	Y	4,452	01/15/2004	01/07/2005
	17	F	Y	4,837	01/16/2004	01/07/2005
	18	F	Y	4,749	01/21/2004	01/07/2005
	19	F	Y	4,784	01/26/2004	01/07/2005
	20	F	F	4,674	01/27/2004	01/07/2005
	21	F	A	4,416	02/19/2004	01/07/2005
	22	F	A	4,468	02/20/2004	01/07/2005
	23	F	A	5,696	10/25/2002	02/26/2003
	24	F	Y	5,491	11/15/2003	04/22/2004
	25	F	Y	4,186	11/07/2002	02/26/2003
	26	F	A	5,237	10/20/2003	03/31/2004
	27	F	A	308	12/01/2004	12/30/2004
	28	F	A	5,137	10/23/2002	03/04/2004
	29	F	A	1,241	01/10/2005	10/22/2005
	30	F	A	4,841	01/19/2005	03/15/2006
east-central Illinois						
	5	F	Y	5,878	01/17/06	06/01/2007
	6	F	A	655	01/05/07	03/04/2007
	14	F	Y	5,396	02/25/06	06/01/2007
	15	F	A	7,360	01/21/08	06/01/2009
	17	F	A	7,670	12/19/07	06/01/2009

Table 3.Continued

Study site	Eartag #	Sex	Age	# of locations	Capture date	End date
east-central Illinois						
	25	F	Y	2,651	01/21/07	06/01/2008
	36	F	A	6,110	12/27/06	06/01/2008
	47	F	Y	5,736	01/29/07	06/01/2008
	48	F	A	5,793	01/21/07	06/01/2008
	49	M	Y	2,578	02/27/08	06/01/2009
	52	F	Y	5,667	01/28/07	06/01/2008
	53	F	Y	5,572	02/02/07	06/01/2008
	56	F	A	5,829	01/23/07	06/01/2008
	61	F	A	5,700	01/27/07	06/01/2008
	62	F	Y	5,751	01/28/07	06/01/2008
	68	F	A	1,883	02/07/07	07/21/2007
	86	M	Y	1,008	03/04/07	06/09/2007
	89	M	F	455	03/14/08	11/14/2008
	111	F	Y	6,827	03/05/08	06/01/2009
	119	F	A	7,309	02/01/08	06/01/2009
	125	F	Y	6,732	03/17/08	06/01/2009
	136	F	A	6,645	03/17/08	06/01/2009

Table 4. Landcover types in the 10 ×10-km southern Illinois study area and the 30 × 130-km east-central Illinois study area. Total areas are in hectares. Percentages are in parenthesis.

Landcover code	southern Illinois	east-central Illinois	Description of cover type
Agriculture	1,405.6(14.1)	25809.4(69.7)	Agricultural fields, mainly corn and soybeans
Aqua[a]	7.5(0.08)	N/A	Aquaculture center
Brush/willow	N/A	452.8(1.2)	Mainly brush and willow trees
Fish[a]	16.0 (0.2)	N/A	Fish hatchery
Forest	5,565.2(55.7)	4878.8(13.2)	Forest consisting mainly of oak-hickory
Grassland	609.9(6.1)	751.1(2.0)	Native grasses, not mowed
Lawn	427.9(4.3)	1135.6(3.1)	Mowed and tended lawns close to buildings
Marsh[a]	13.9(0.1)	N/A	Marsh
Noveg	N/A	53.3(0.1)	No Vegetation. Graveled driveways, parking lots etc.
Oldfield	136.7(1.4)	105.2(0.3)	Field in late successional state, with brush and trees
Pasture	442.6(4.4)	368.5(1.0)	Grassy fields, grazed by livestock
Rail	N/A	23.0(0.1)	Rail road
Road	80.0 (0.8)	305.0(0.8)	Highways, roads and gravel roads
Sand/beach	N/A	117.0(0.3)	Sandy areas and beach
Urban	117.7(1.2)	518.4(1.0)	Buildings and houses
Water	1,181.2(11.8)	2511.5(6.8)	Lakes, ponds, and rivers

Table 5. Prior distributions for movement models fitted to location data from GPS collars deployed on white-tailed deer captured in the southern Illinois study area, winter 2002-2006 and the east-central Illinois study area, winter 2006-2009.

Parameter	Prior distribution	Interpretation
a_i	Gamma(1, 0.1)	Scale parameter for Weibull distribution describing step length for the *i*th movement state
eps_i	Gamma(1, 0.1)	Difference between a_i and a_i+1 when multiple walks fitted ($a_i+1 = a_i + \mathrm{eps}_\mathrm{i}$)
b_i	Gamma(1, 0.1)	Shape parameter for Weibull distribution describing step length for the *i*th movement state
μ_i	Uniform(π,π)	Mean direction for turning angles for the *i*th movement state
p_i	Uniform(0, 1)	Mean cosine for turning angles for the *i*th movement state
$\eta_{1,t}$	Uniform(0, 1)	Probability that the animal is in movement state 1 at time *t* ($\eta_{2,t} = 1-\eta_{1,t}$)
v_h	Normal(0, σ), σ = 100	Coefficients in equation (3) relating state of individual to habitat in which it currently resides
β_1	Normal(0, σ), σ = 100	Intercept in equation (4) relating probability of switching to distance to open habitat
m	Normal(0, σ), σ = 100	Slope in equation (4) relating probability of switching to distance to open habitat
q_{ij}	Uniform(0, 1)	Transition probability from movement state *i* to *j*

Table 6. Landcover types in the 10 ×10-km and 10 × 10-km southern Illinois study area and east-central Illinois study area respectively. Total areas are in hectares. Percentages can be obtained by dividing total areas by 100.

Landcover code	southern Illinois	east-central Illinois	Description of cover type
Agriculture	1,405.6	6,984.0	Agricultural fields, mainly corn and soybeans
Aqua[a]	7.5	N/A	Aquaculture center
Brush/willow	N/A	252.4	Mainly brush and willow trees
Fish[a]	16.0	N/A	Fish hatchery
Forest	5,565.2	1,380.5	Forest consisting mainly of oak-hickory
Grassland	609.9	264.6	Native grasses, not mowed
Lawn	427.9	203.0	Mowed and tended lawns close to buildings
Marsh[a]	13.9	N/A	Marsh
Noveg	N/A	12.4	No Vegetation. Graveled driveways, parking lots etc.
Oldfield	136.7	49.9	Field in late successional state, with brush and trees
Pasture	442.6	106.5	Grassy fields, grazed by livestock
Rail	N/A	2.1	Rail road
Road	80.0	72.5	Highways, roads and gravel roads
Sand/beach	N/A	29.1	Sandy areas and beach
Urban	117.7	15.7	Buildings and houses
Water	1,181.2	630.9	Lakes, ponds, and rivers

Table 7. Demographic parameters used in DeerLandscapeDisease. CFL = contiguous, forest landscape, FFL = fragmented forest landscape.

Parameter/state	Value	Source
Chance of dispersal	Males: 0.7 Females: 0.2	Hawkins et al. 1971,Nixon et al. 1994, Rosenberry et al. 1999, Nixon et al. 2007
Chance of exploratory movement	Gestation: 0.02 Rut: 0.02	Estimated from field data (Kjær et al. 2009, unpublished data)
Gestation time	187-222 days	Marchinton and Hirth 1984
Group adhesion	Males: 0.60 Females:0.95	Added in model to account for male groups being more fluid than female
Maximum group size (adults)	Males: 10 Females: 4	Marchinton and Hirth 1984
Maximum home range size (ha)	CFL: 217.78 FFL: 216.86	Calculated from field data
Minimum forest proportion in home range	CFL: 0.19 FFL: 0.22	Calculated from field data
Minimum home range size (ha)	CFL: 6. 46 FFL: 5.34	Calculated from field data
Number of fawns born to each female (proportions)	1 fawn: 0.25 2 fawns: 0.50 3 fawns: 0.25	Verme and Ullrey 1984
Yearly mortality	Males: 0.40 Females: 0.20 Fawns: 0-2 months: 0.44 Fawns: 2-12 months: 0.20	Hawkins et al. 1970, Nixon et al. 1991, Nixon et al. 1994, Rohm et al. 2007

Table 8. Movement parameters used in DeerLandscapeDisease. CFL = contiguous forest landscape, FFL = fragmented forest landscape.

Parameter/state	Distributions	Distribution parameter values	Source
Follower deer distance to leader	Exponential	Gestation: $\lambda = 0.00442$ Fawning: $\lambda = 0.00331$ Prerut: $\lambda = 0.00317$ Rut: $\lambda = 0.00406$ Fawns: $\lambda = 0.1$ Mating movement males: $\lambda = 0.1$	Fitted to field data
Movement step lengths	Weibull	Parameters a and b drawn from following normal distributions based on the variation in animals analyzed in the data sets: CFL: Gestation: a: X~N (6.595, 1.551), b: X~N (0.866, 0.201) Fawning: a: X~N (6.919, 1.866), b: X~N (0.895, 0.185) Prerut: a: X~N (5.582, 1.640), b: X~N (0.888, 0.101) Rut: a: X~N (6.026, 1.377), b: X~N (0.823, 0.133) FFL: Gestation: a: X~N (4.166, 0.949), b: X~N (0.770, 0.169) Fawning: a: X~N (4.899, 1.362), b: X~N (0.828, 0.148) Prerut: a: X~N (4.841, 1.257), b: X~N (0.801, 0.116) Rut: a: X~N (4.918, 1.868), b: X~N (0.808, 0.173)	Fitted to field data (Morales et al. 2004)

Table 8. Continued

Parameter/state	Distributions	Distribution parameter values	Source
Movement turn angle	Wrapped Cauchy	Parameters μ and ρ drawn from the following normal distributions based on the variation in animals analyzed in the data sets::	Fitted to field data (Morales et al. 2004)
		CFL: Gestation: μ: $X \sim N(0.455, 1.753)$, ρ: $X \sim N(0.051, 0.037)$ Fawning: μ: $X \sim N(1.252, 2.078)$, ρ: $X \sim N(0.071, 0.034)$ Prerut: μ: $X \sim N(1.238, 1.563)$, ρ: $X \sim N(0.087, 0.051)$ Rut: μ: $X \sim N(1.829, 1.346)$, ρ: $X \sim N(0.075, 0.039)$	
		FFL: Gestation: μ: $X \sim N(0.455, 1.753)$, ρ: $X \sim N(0.051, 0.037)$ Fawning: μ: $X \sim N(1.252, 2.078)$, ρ: $X \sim N(0.071, 0.034)$ Prerut: μ: $X \sim N(1.238, 1.563)$, ρ: $X \sim N(0.087, 0.051)$ Rut: μ: $X \sim N(1.829, 1.346)$, ρ: $X \sim N(0.075, 0.039)$	
		Dispersal/Exploratory movement: $\mu = 0.02$, $\rho = 0.99$	Straight-line movement

Table 9. Pearson correlation coefficients of force of infection at year *t* against prevalence (P) or density (D) of infectious deer (infected >6 months) at years *t*, *t*-1, and *t*-2 in DeerLandscapeDisease, with scenarios differing by mode of transmission, landscape structure, and maximum group size.

Scenario			Predictor					
Transmission	Landscape	Group Size	$P_{inf,t}$	$P_{inf,t-1}$	$P_{inf,t-2}$	$D_{inf,t}$	$D_{inf,t-1}$	$D_{inf,t-2}$
Direct	Fragmented	Default	0.71	..	..	0.71	..	..
Direct	Fragmented	Reduced	0.71	..	..	0.75	..	..
Direct	Contiguous	Default	0.84	..	..	0.88	..	..
Direct	Contiguous	Reduced	0.84	..	..	0.87	..	..
Indirect	Fragmented	Default	0.62	0.57	0.35	0.60	0.70	0.53
Indirect	Contiguous	Default	0.32	0.61	0.29	0.42	0.62	0.35

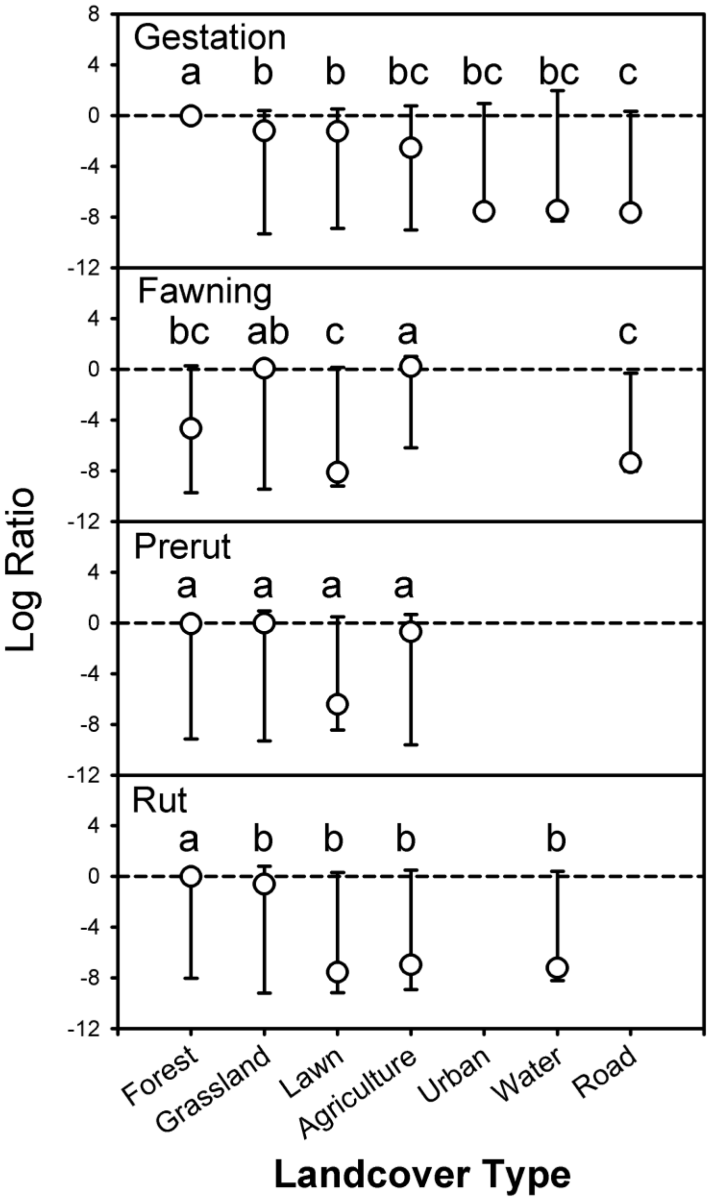

Figure 1. Log ratios, log(contact landcover/available landcover), for gestation fawning, prerut and rut seasons. Values are medians and their respective 10th and 90th percentiles. A positive log ratio for a given land cover type indicates greater contact rates than expected on the basis of availability. For each season, land cover types sharing a letter did not have statistically different (α = 0.05) log ratios based on Tukey's multiple range test.

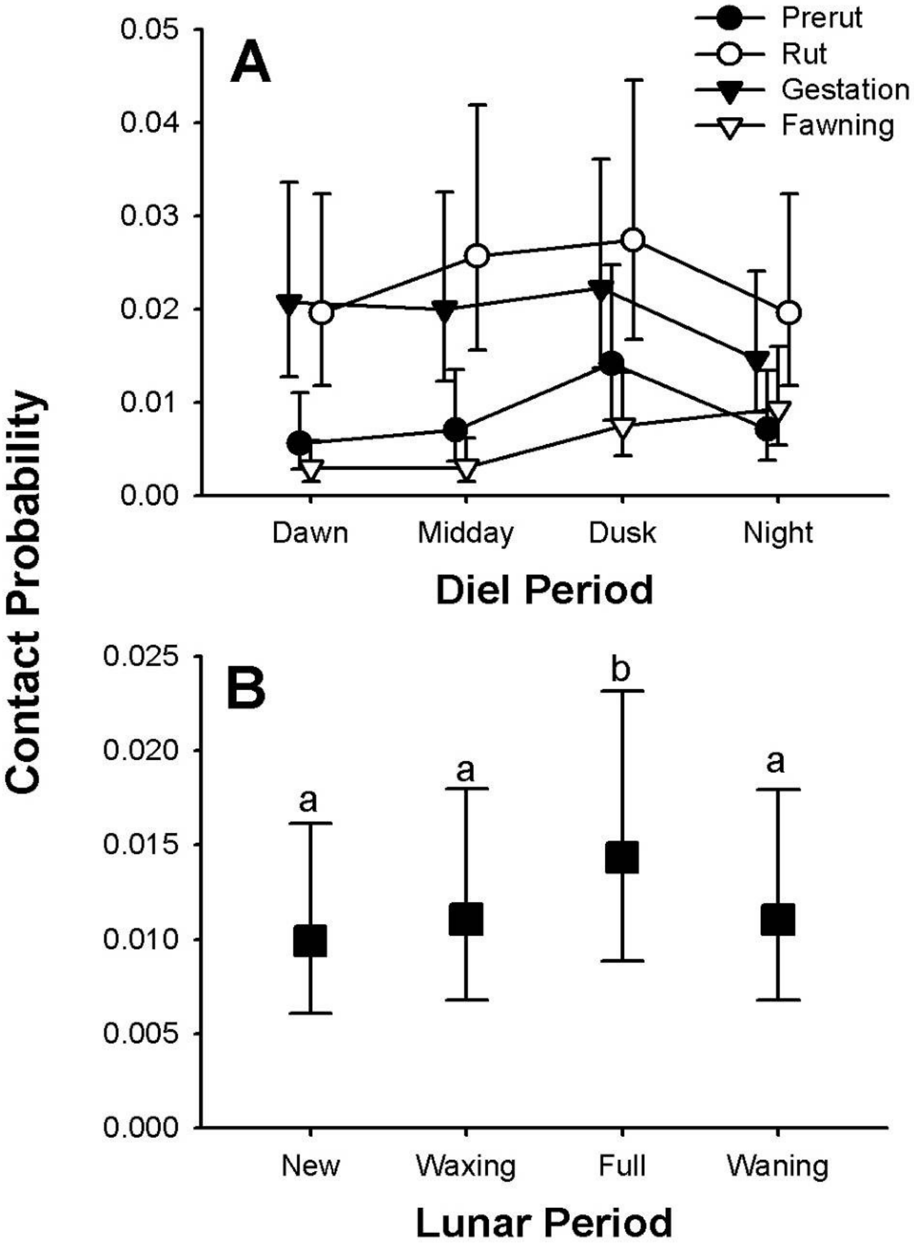

Figure 2. Contact probabilities for (a) seasons and diel periods, and (b) lunar periods. In (b), periods sharing a letter did not have statistically different (α = 0.05) contact rates based on Tukey's multiple range test.

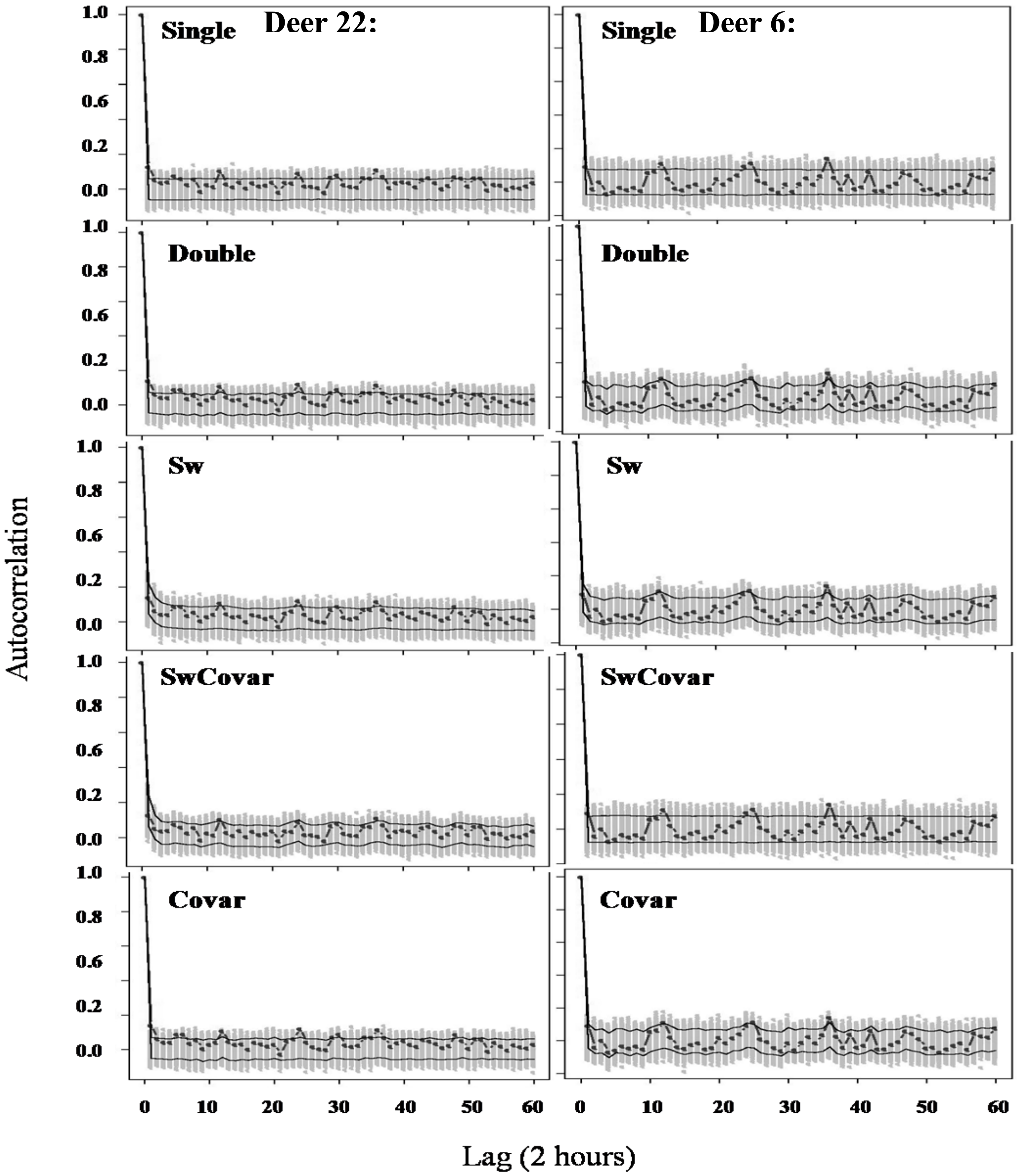

Figure 3. Autocorrelation functions (acfs) of bi-hourly movement rate for observed and modeled deer paths for lags 1-60 for the gestation season. Depicted are deer 22 from the southern Illinois study sites and deer 6 from the east-central Illinois study site. Thick, black dotted lines are observed acfs. Thin lines are 95% credibility intervals for the acfs of modeled paths (5000 replicates). Gray dots are autocorrelation values for modeled paths.

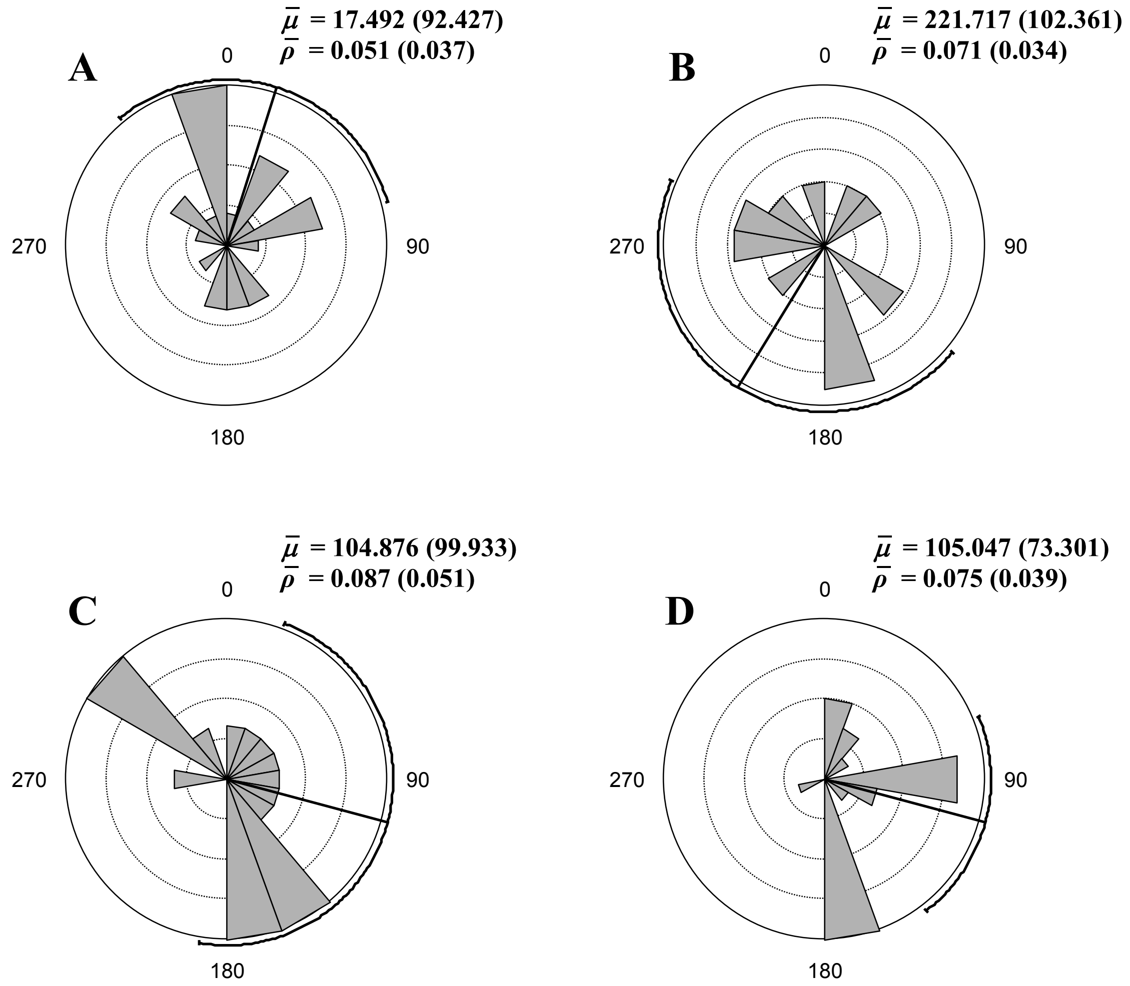

Figure 4. Turn angle distributions for the single model fitted to movement data from the southern Illinois study site. Mean values of wrapped Cauchy distribution parameters μ (mean angle) and ρ (mean cosine) are calculated from posterior distributions, with standard deviations (in parentheses) among individual deer. A) gestation (n = 27 deer), B) fawning (n = 20 deer) , C) prerut (n = 19 deer) and D) rut (n = 25 deer). The black line running from the center of the diagram to the outer edge denotes the mean angle and the arcs extending to either side represent the 95% confidence limits of the mean.

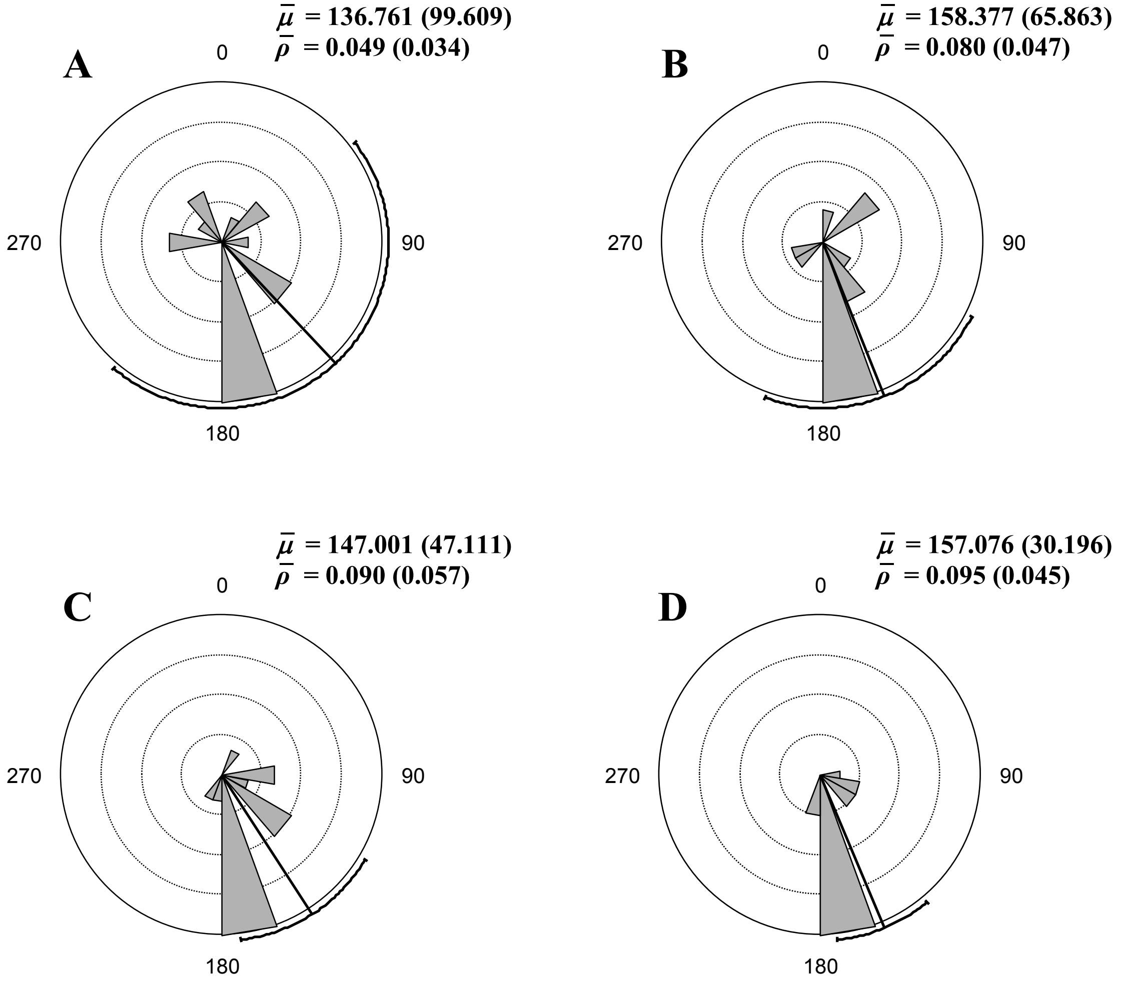

Figure 5.Turn angle distributions for the single model fitted to movement data from the east-central Illinois study site. Mean values of wrapped Cauchy distribution parameters μ (mean angle) and ρ (mean cosine) are calculated from posterior distributions, with standard deviations (in parentheses) among individual deer A) gestation (n = 20 deer), B) fawning (n = 19 deer) , C) prerut (n = 18 deer) and D) rut (n=18 deer). The black line running from the center of the diagram to the outer edge denotes the mean angle and the arcs extending to either side represent the 95% confidence limits of the mean.

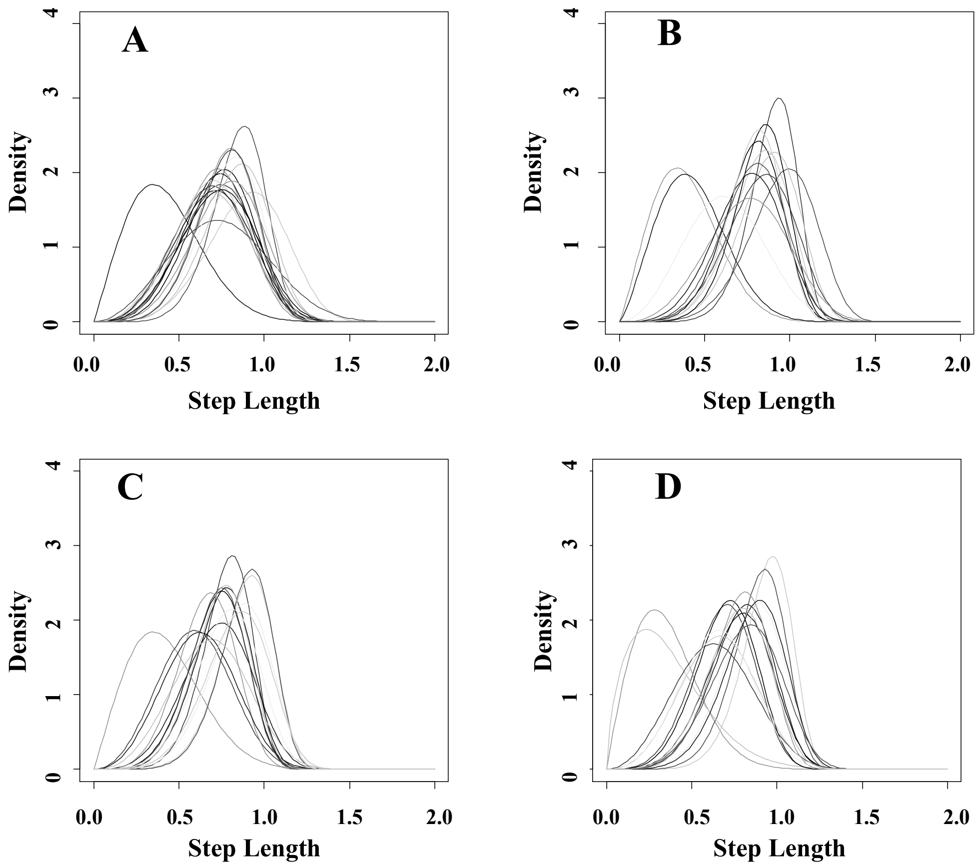

Figure 6. Weibull distributions of step lengths for the single model (1 correlated random walk) fitted to movement data from the southern Illinois study site. A) gestation (n = 27 deer), B) fawning (n = 20) , C) prerut (n = 19) and D) rut (n=25). Distributions drawn are based on mean values of parameters (*a* and *b*) from their posterior distributions.

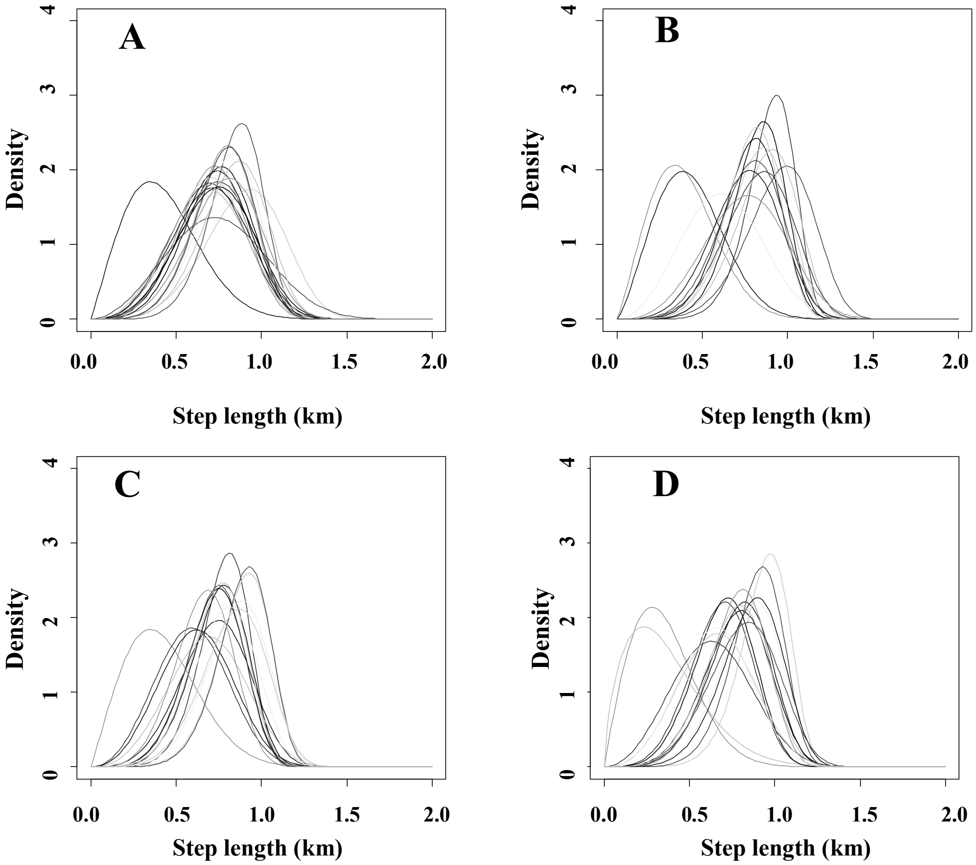

Figure 7. Weibull distributions of step lengths for the single model (1 correlated random walk) fitted to movement data from the east-central Illinois study site. A) gestation (n = 20), B) fawning (n = 19) , C) prerut (n = 18) and D) rut (n=18). Distributions drawn are based on mean values of parameters (*a* and *b*) from their posterior distributions.

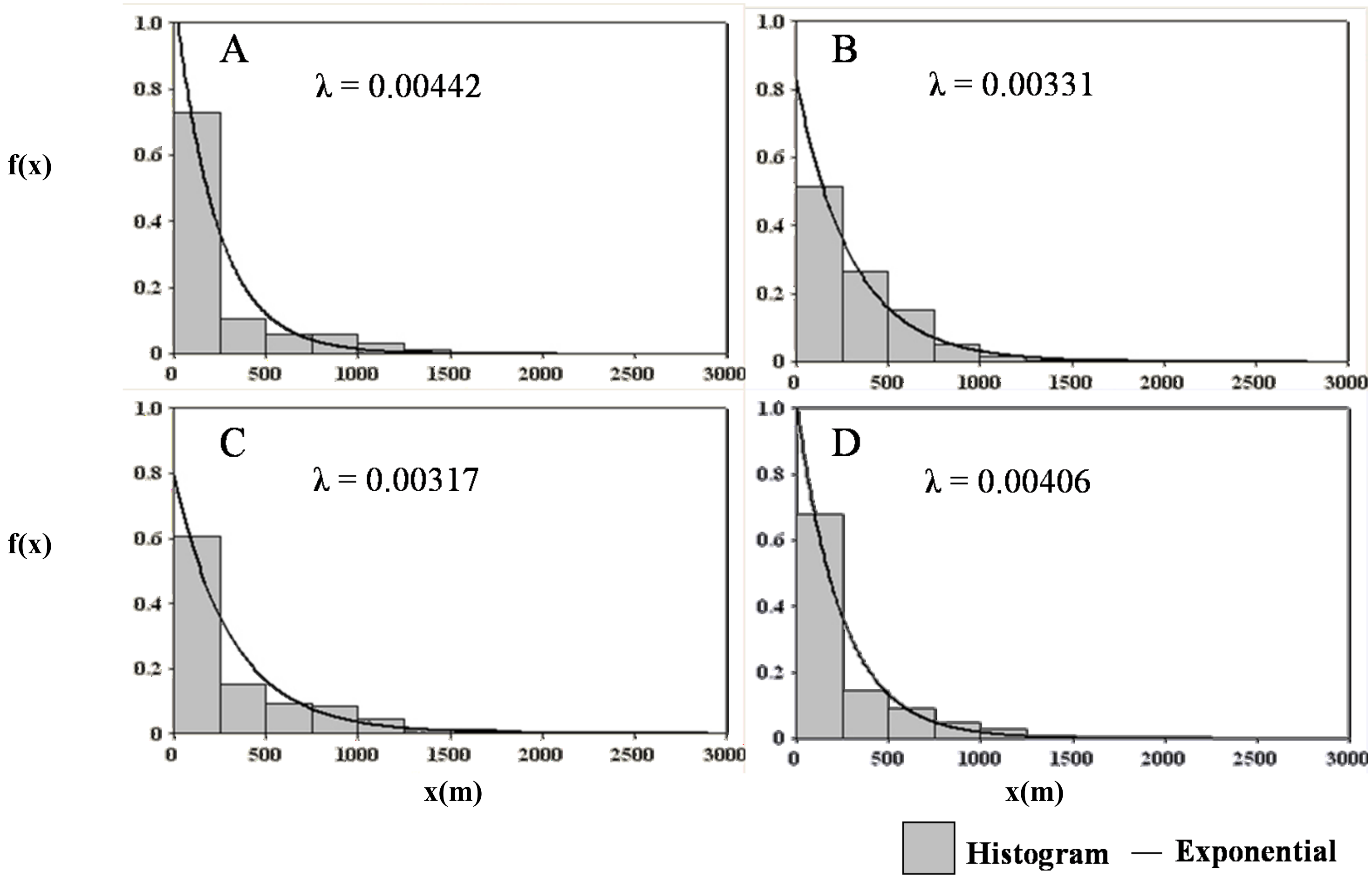

Figure 8. Exponential probability density functions fitted to group-member distances from the southern Illinois and east-central Illinois study sites. A) gestation (n = 7806 simultaneous location pairs), B) fawning (n = 5143), C) prerut (n=2790) and D) rut (n = 3978).

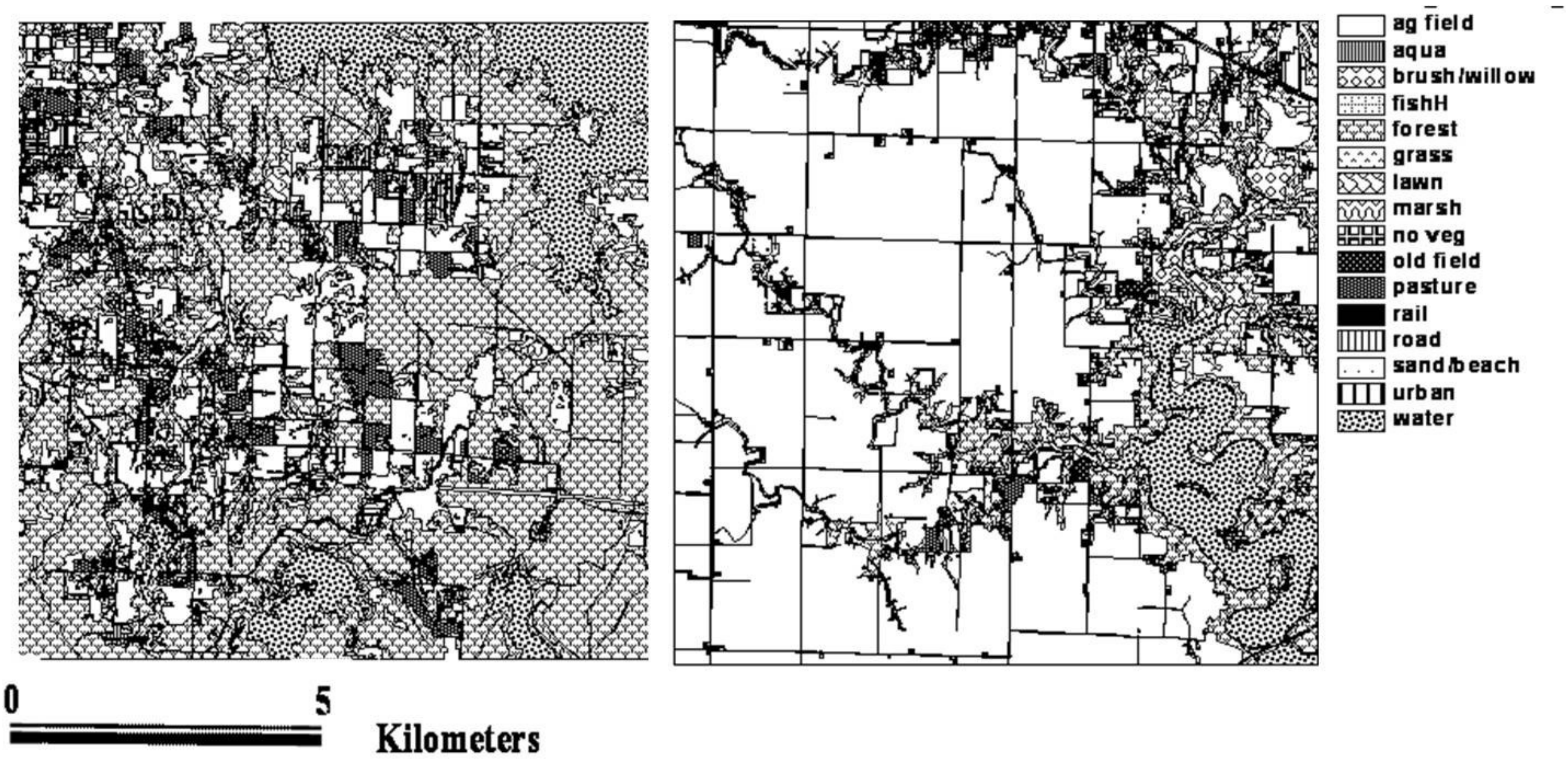

Figure 9. Landcover composition of 10x10 km areas of the southern Illinois and east-central Illinois study sites respectively.

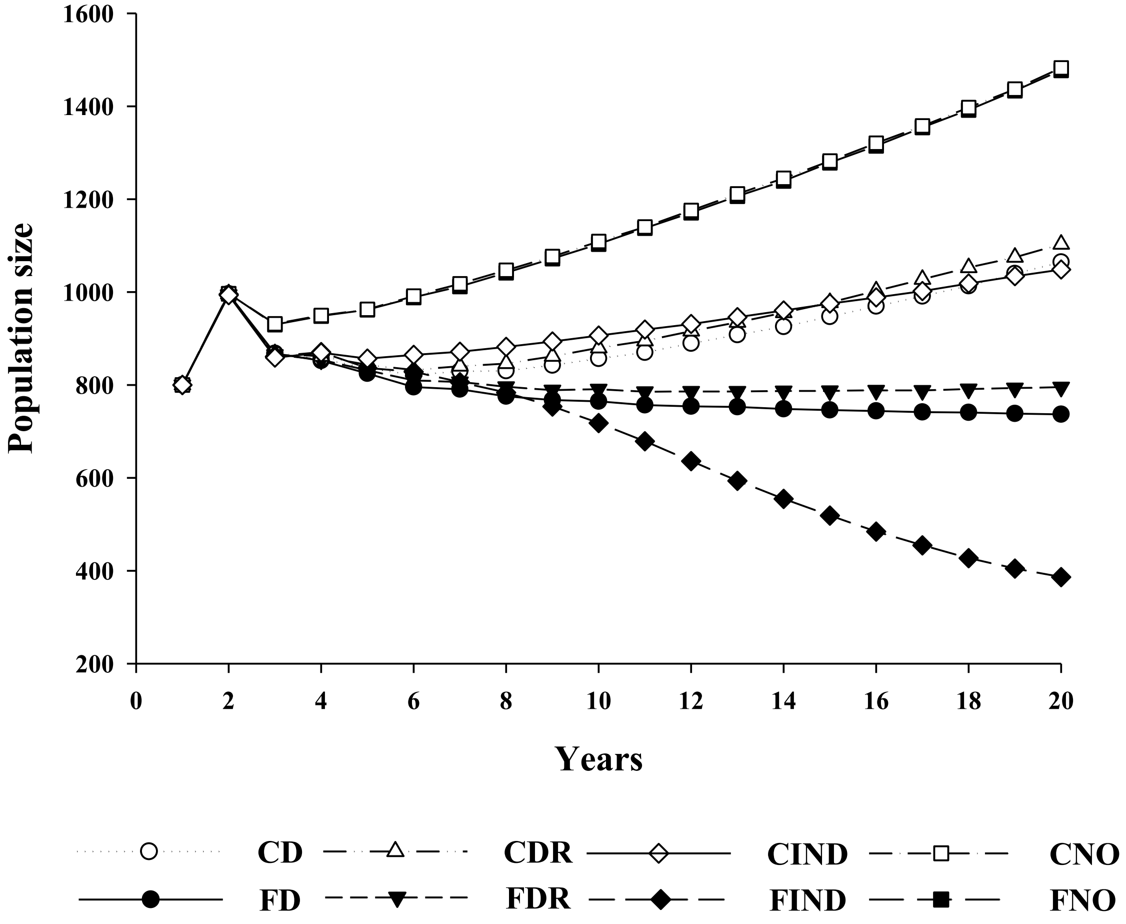

Figure 10. Average deer population sizes in DeerLandscapeDisease. F = fragmented forest, C = contiguous forest, D = direct transmission, R = reduced group size, IND = indirect transmission, and NO = no disease. N = 600 for each scenario. FNO is obscured and falls beneath CNO.

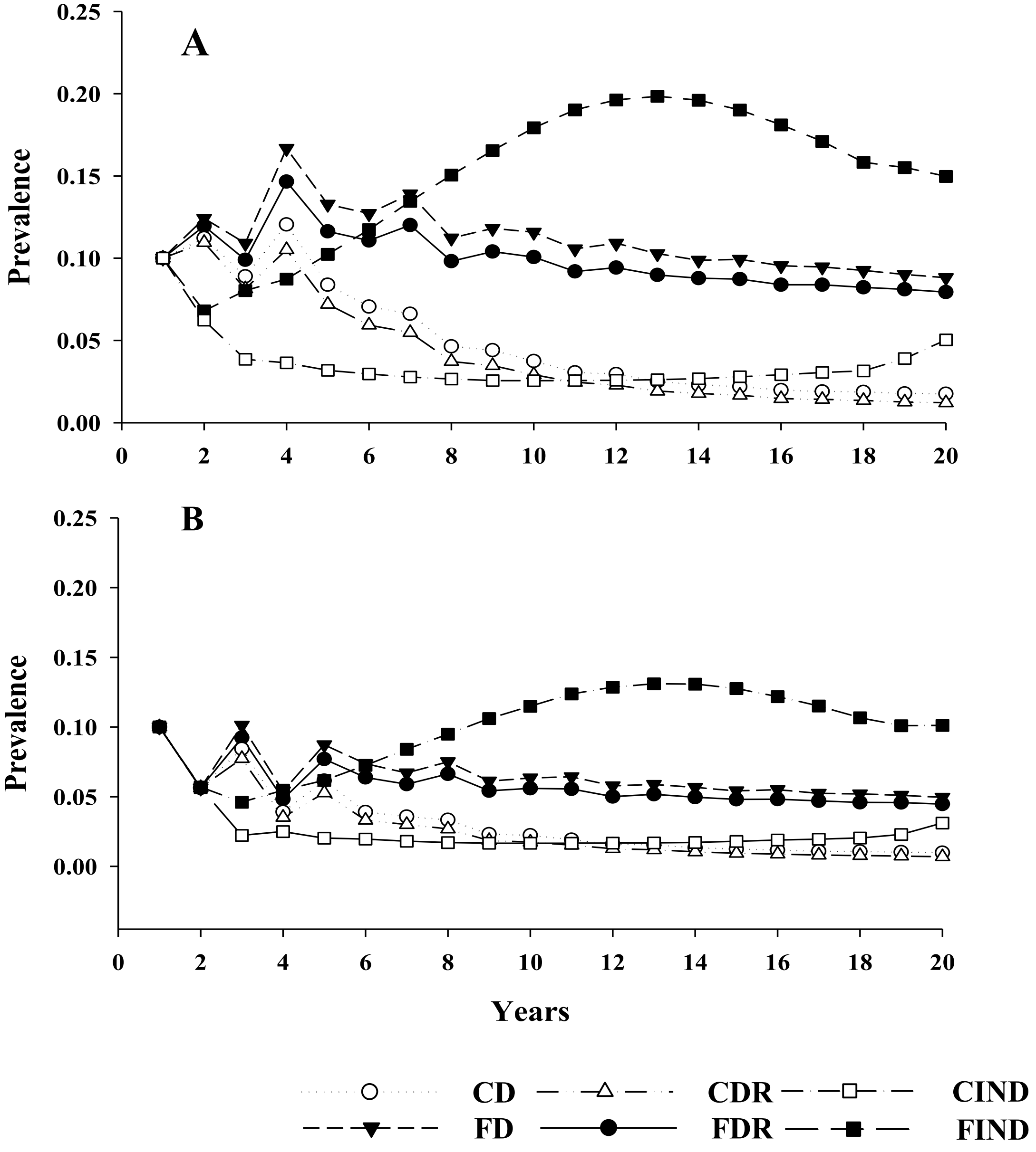

Figure 11. Average values for total prevalence in DeerLandscapeDisease scenarios for A) all infected individuals in the population B) individuals infected >6 months. F = fragmented forest, C = contiguous forest, D = direct transmission, R = reduced group size, and IND = indirect transmission. N = 600 for each scenario.

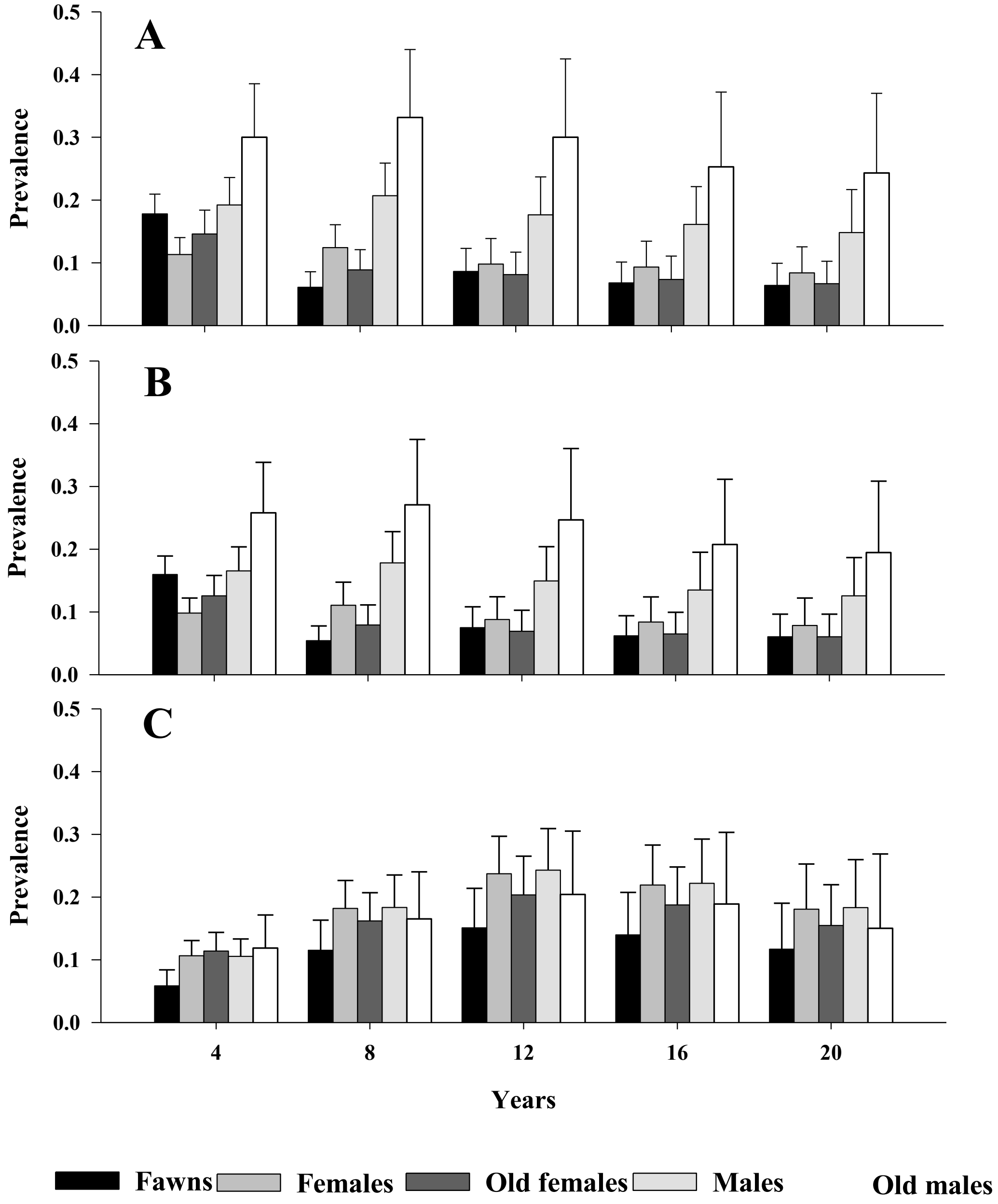

Figure 12. Infection prevalence divided into age and sex groups in the fragmented forest landscape within an individual-based simulation of chronic wasting disease transmission. A) direct transmission, B) direct transmission, reduced group size, and C) indirect transmission. Error bars are standard errors. For illustrative purpose, only years 4, 8, 12, 16 and 20 are depicted.

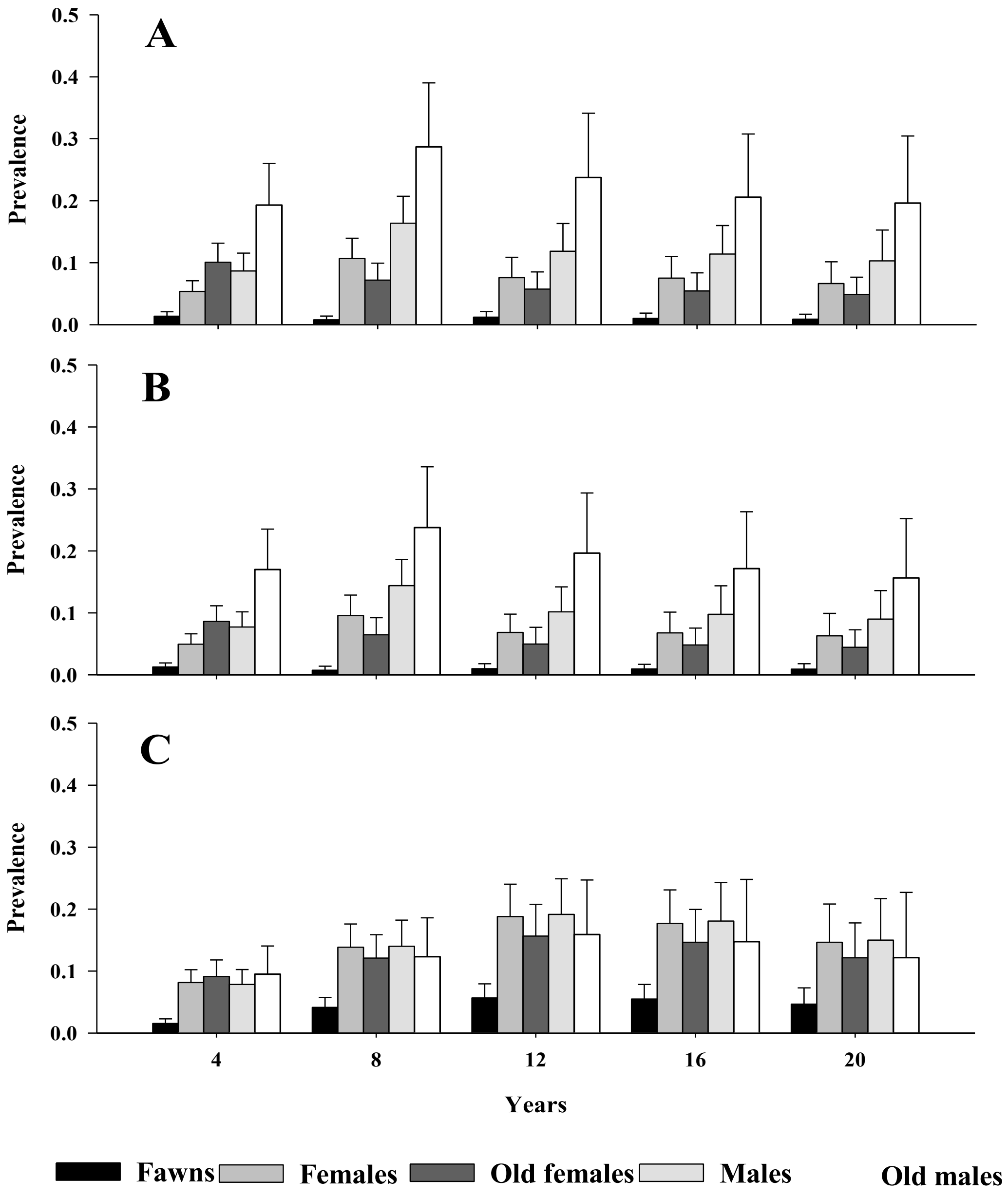

Figure 13. Prevalence of infectious individuals (infected longer than 6 months) divided into age and sex groups in the fragmented forest landscape within an individual-based simulation of chronic wasting disease transmission. A) direct transmission, B) direct transmission, reduced group size, and C) indirect transmission. Error bars are standard errors. For illustrative purpose, only years 4, 8, 12, 16 and 20 are depicted.

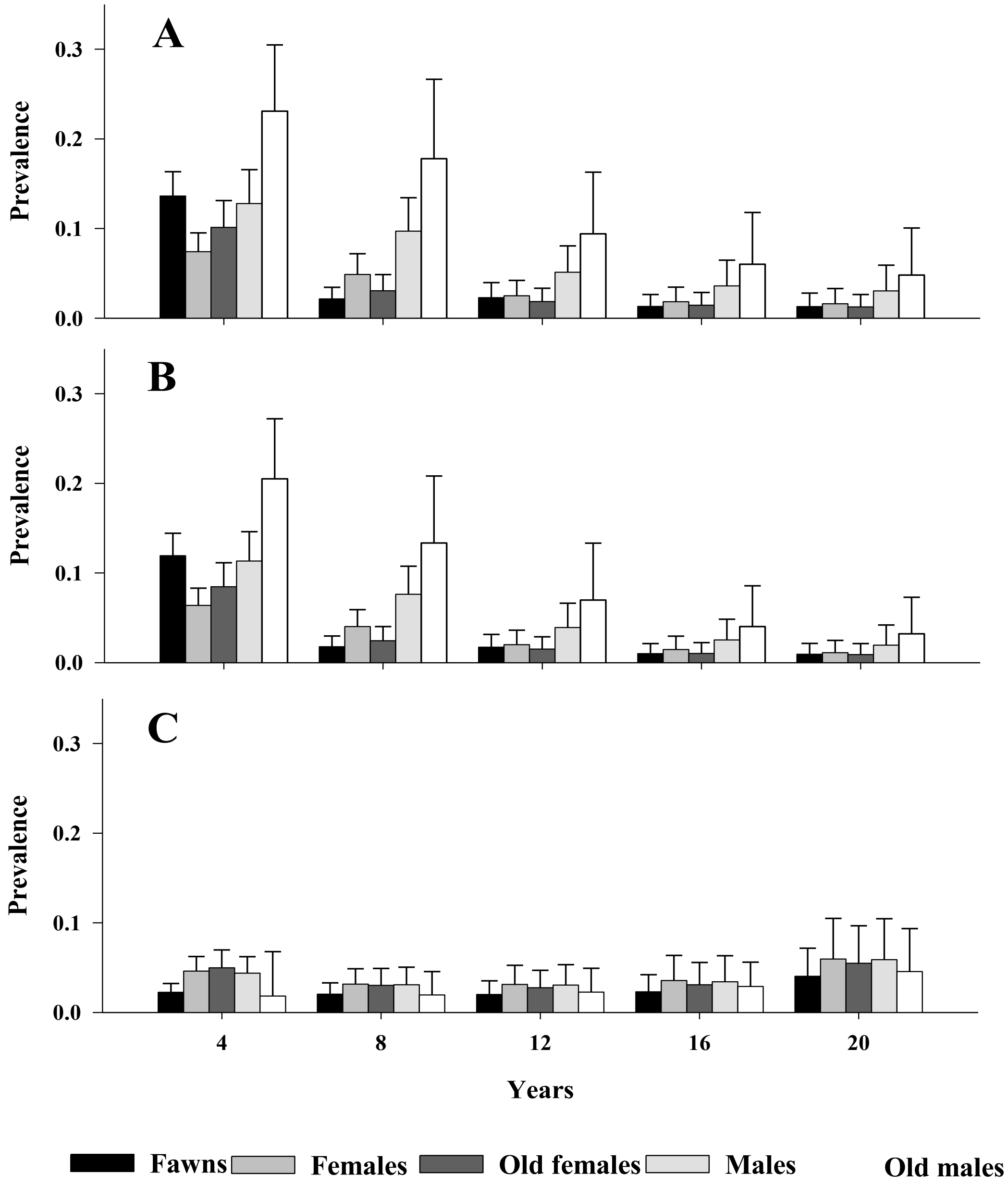

Figure 14. Infection prevalence by age and sex groups in the contiguous forest landscape within an individual-based simulation of chronic wasting disease transmission. A) direct transmission, B) direct transmission, reduced group size, and C) indirect transmission. Error bars are standard errors. For illustrative purpose, only years 4, 8, 12, 16 and 20 are depicted.

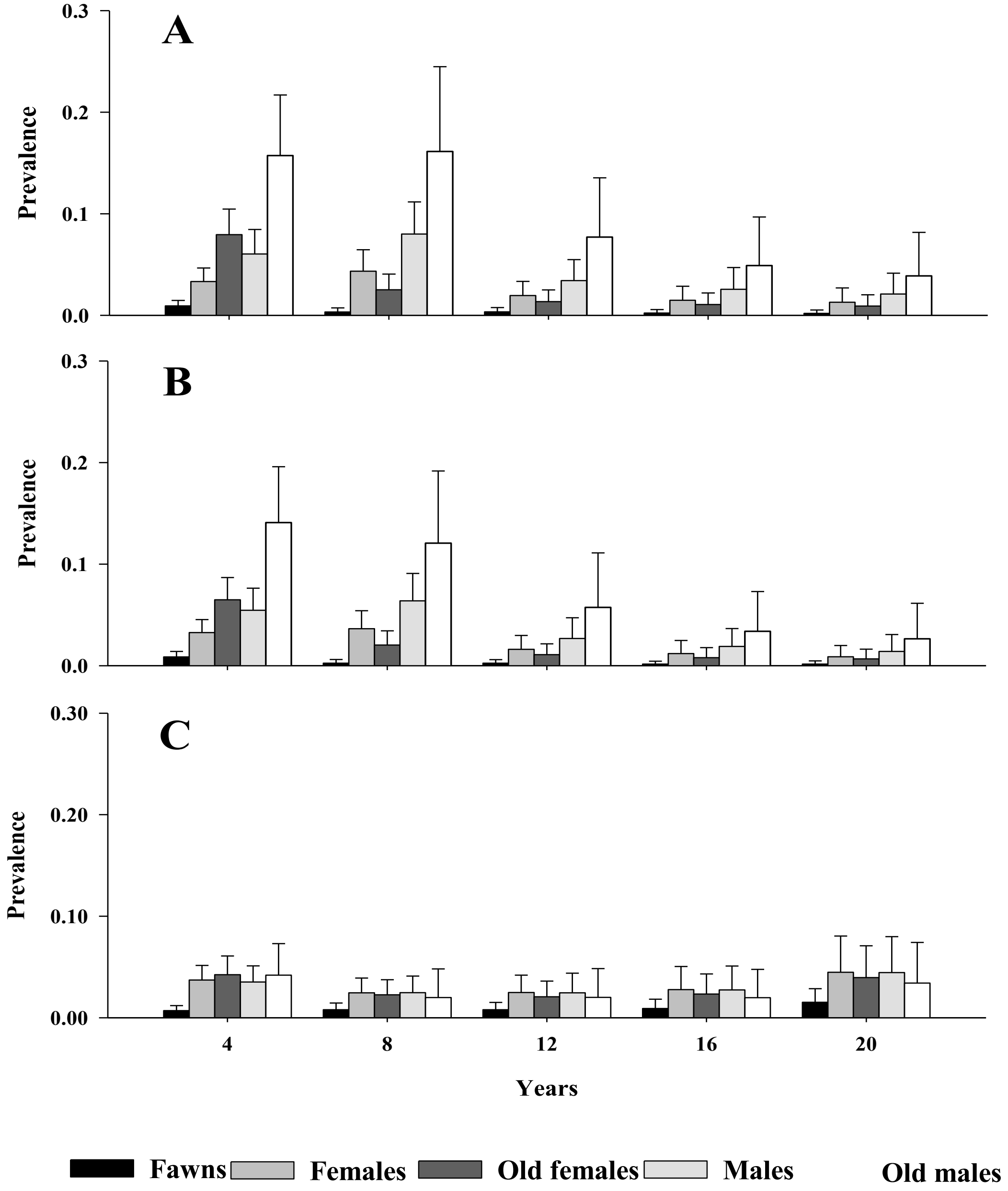

Figure 15. Prevalence of infectious individuals (infected longer than 6 months) by age and sex groups in the fragmented forest landscape within an individual-based simulation of chronic wasting disease transmission. A) direct transmission, B) direct transmission, reduced group size, and C) indirect transmission. Error bars are standard errors. For illustrative purpose, only years 4, 8, 12, 16 and 20 are depicted.

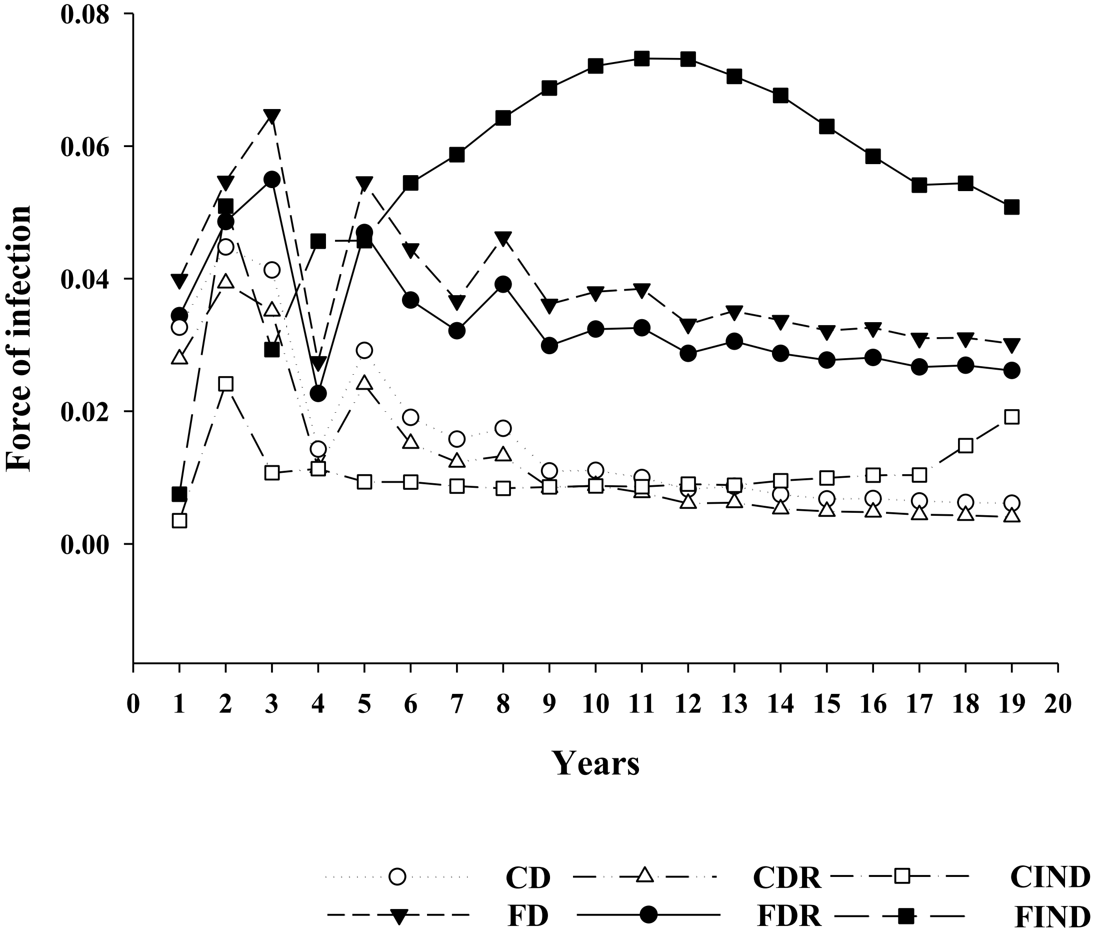

Figure 16. Average values for the force of infection in DeerLandscapeDisease scenarios. F = fragmented forest, C = contiguous forest, D = direct transmission, R = reduced group size, and IND = indirect transmission. N = 600 for each scenario.

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APPENDICES

APPENDIX A

Deviance Information Crition (DIC) values for all 4 seasons and all 5 models for the southern Illinois study area (2002-2006) and east-central Illinois study area (2006-2008) respectively. "sw" indicates the double model with switch, "swcovar" is the double switch with covariates model and "covar" is the double with covariates model. "nc" means non-convergence.

A.1. Southern Illinois, gestation

Deer no.	single	double	sw	swcovar	covar
1	58994.04	nc	nc	nc	nc
2	21574.13	21948.65	nc	21820.45	21890.22
3	21364.26	nc	nc	21170.02	nc
4	21053.81	nc	nc	22171.85	nc
6	32444.16	nc	nc	32574.34	34310.5
7	32764.04	32531.47	33019.81	32454.77	nc
8	28814.05	nc	nc	30945.95	nc
9	28724.59	30577.2	nc	30285.5	nc
10	29284.28	27227	30015.8	28495.29	nc
11	28362.13	28392.35	nc	28056.53	nc
12	34934.19	nc	nc	35480.91	nc
13	51824.22	nc	nc	53273.7	nc
14	43084.02	nc	nc	nc	48204.5
15	50272.82	nc	nc	nc	nc
16	23244.21	24200.48	nc	nc	nc
17	24413.45	25624.07	nc	25835.43	25628.87
18	20343.01	26083.96	nc	29864.72	26231.05
19	22553.09	28105.81	24804.82	22758.41	nc
20	20022.97	27599.25	25824.09	nc	26654.05
21	17553.16	19720.79	20436.34	22060.08	nc
22	17633.125	19647.01	21773.91	19574.9	19499.95
23	38173.04	40443.75	42581.21	40624.23	40574.39
25	27132.99	34506.45	30996.31	42948.41	35592.05
26	38513.99	43078.88	45162.82	43121.21	43460.5
28	39363.32	44409.38	54586.05	89747.62	nc
30	36413.61	42913.13	42962.61	40642.01	43371.13

A.2. Southern Illinois, fawning

Deer no.	single	double	sw	swcovar	covar
1	40004.17	nc	43350.61	41356.45	41936.08
6	28854.16	33809.61	32511.45	32250.80	32617.76
7	29084.58	nc	nc	30201.85	nc
8	26044.22	27343.98	nc	nc	27476.27
9	26444.15	nc	nc	nc	nc
13	41224.04	43719.53	nc	44018.71	44627.09
16	20494.01	30793.41	24767.44	22231.61	30193.62
17	20503.75	24656.28	nc	nc	nc
18	20704.16	22736.72	nc	23132.36	21889.46
19	20223.00	22181.32	21433.16	21943.33	21627.10
20	20783.14	21424.13	20988.51	21583.07	22027.22
21	20695.01	21739.81	22344.86	22170	22060.62
22	20554.23	23338.44	22863.49	nc	nc
23	21414.34	nc	nc	22095.75	nc
24	19484.26	35992.85	nc	22147.63	nc
25	20633.46	21174.97	nc	21327.51	21290.00
26	20334.25	nc	nc	nc	nc
28	20714.44	21881.72	nc	nc	nc
29	21223.73	23809.95	22800.13	22548.15	24103.21
30	20663.99	30008.05	nc	23538.34	28396.42

A.3. Southern Illinois, prerut

Deer no.	single	double	sw	swcovar	covar
1	25253.90	nc	nc	nc	25831.26
2	1128.25	1194.66	1214.26	1337.87	1530.65
10	12483.32	nc	nc	12372.28	nc
11	8225.19	8416.92	nc	8289.00	8361.76
12	3029.97	3401.01	3055.31	3257.55	3376.41
13	12023.91	nc	nc	13180.08	nc
16	12334.30	13726.42	14622.15	nc	3595.28
17	12444.39	21001.22	nc	12981.25	nc
18	12623.74	14622.32	14957.36	14477.18	nc
19	11783.67	12727.92	nc	12666.01	12781.31

A.3. Continued

Deer no.	single	double	sw	swcovar	covar
20	12813.93	13502.00	13721.24	13509.50	nc
21	12814.02	13401.85	nc	13991.58	nc
22	13133.65	13721.48	13701.95	nc	13712.40
23	12914.10	nc	nc	13324.91	nc
24	11623.07	17023.01	12139.87	12506.95	16257.54
25	12253.83	nc	nc	nc	nc
26	12014.36	12707.26	13135.91	14471.74	12821.48
28	11913.21	12273.98	nc	12402.49	12291.35
30	11973.79	14469.56	14931.60	15907.25	14151.99

A.4. Southern Illinois, rut

Deer no.	single	double	sw	swcovar	covar
1	47604.08	nc	nc	nc	nc
2	23654.22	nc	nc	24714.53	25506.08
3	22624.19	nc	nc	22640.45	60752.41
4	19394.18	nc	nc	20047.82	nc
5	4418.22	4495.64	nc	4959.38	nc
10	23754.04	nc	nc	23607.01	nc
11	23133.81	23788.13	nc	nc	nc
12	23474.28	nc	nc	24876.40	nc
13	19354.18	nc	20145.64	19936.48	nc
14	16513.97	18346.82	16441.96	18945.09	nc
15	8473.96	8883.22	nc	nc	8976.36
16	18653.60	nc	nc	nc	nc
17	23203.91	25003.73	27024.24	24329.19	nc
18	24043.39	nc	nc	nc	nc
19	22693.95	nc	nc	22782.91	nc
20	23693.14	nc	nc	23959.57	nc
21	23254.23	23944.11	nc	nc	nc
22	23624.11	nc	nc	24214.65	24933.00
23	24704.19	nc	nc	nc	nc
24	23484.24	nc	nc	nc	26561.92

A.4. Continued

Deer no.	single	double	sw	swcovar	covar
25	13634.13	nc	13663.65	nc	nc
26	20504.27	nc	20458.91	nc	nc
27	5200.12	6118.62	6473.81	7135.22	6341.55
28	16984.20	18101.09	20496.90	29684.50	18067.57
30	12514.32	13004.45	nc	nc	nc

A.5. East-central Illinois, gestation

Deer no.	single	double	sw	swcovar	covar
5	51013.69	53970.41	nc	52908.40	nc
6	11453.82	11918.78	13491.92	11977.91	11738.8
14	42074.52	46727.25	45033.81	44136.39	nc
15	54643.56	55819.28	46879.16	nc	nc
17	12384.90	nc	nc	nc	nc
25	12294.36	13475.92	15023.66	13140.00	13635.63
36	nc	nc	trap	nc	62008.65
47	nc	49467.25	47557.75	nc	nc
48	51875.06	nc	nc	55201.13	nc
49	9401.12	nc	nc	nc	14119.12
52	48663.92	60355.92	nc	nc	nc
53	47852.92	nc	56418.88	48690.37	nc
56	49784.39	51956.13	nc	51272.92	nc
61	49904.43	nc	nc	nc	nc
62	49443.51	53838.45	nc	nc	51495.38
68	19294.31	21017.78	19805.36	20090.94	nc
86	13533.70	13938.90	15135.81	13847.27	13817.20
89	7759.02	8084.14	7253.72	nc	8167.10
111	12004.02	50096.05	nc	41338.66	49466.08
119	49143.09	53538.00	nc	49594.91	nc
125	38153.25	43276.08	35761.8	39014.45	41982.95
136	38744.41	42337.01	nc	39805.78	nc

A.6. East-central Illinois, fawning

Deer no.	single	double	sw	swcovar	covar
5	24893.58	27342.30	nc	nc	nc
14	24184.21	nc	nc	nc	26135.23
15	55464.38	56710.06	nc	nc	nc
17	54874.32	nc	nc	nc	nc
25	12554.96	12391.62	12629.31	nc	13270.28
36	12554.78	nc	nc	nc	nc
47	nc	25914.61	nc	nc	nc
48	25363.99	33312.00	nc	nc	nc
49	18363.02	nc	nc	nc	nc
52	24644.06	nc	nc	nc	29539.68
53	24353.78	25730.61	25029.68	25066.94	26480.21
56	24774.06	27681.77	29301.81	nc	nc
61	25254.20	24654.42	nc	25559.26	nc
62	24744.32	25125.87	nc	25233.04	25425.36
68	12794.24	nc	nc	nc	nc
86	4000.39	4189.46	4543.38	4136.45	4206.60
111	52659.78	nc	nc	nc	nc
119	53353.02	nc	nc	53973.75	nc
125	50884.24	nc	55268.88	nc	54235.10
136	51724.31	nc	60529.45	nc	nc

A.7. East-central Illinois, prerut

Deer no.	single	double	sw	swcovar	covar
5	12073.63	nc	3696.76	13016.60	13110.16
14	11744.64	nc	nc	nc	nc
15	12902.92	nc	nc	nc	nc
17	12384.52	nc	nc	nc	13675.28
25	9439.91	13506.68	nc	9686.25	12886.73
36	11993.84	12759.73	11890.10	nc	nc
47	12094.21	13962.49	nc	12449.66	13574.06
48	11954.01	112848.09	nc	nc	nc

A.7. Continued

Deer no.	single	double	sw	swcovar	covar
49	9401.12	nc	nc	11069.24	8873.01
52	11896.93	nc	12833.41	nc	11109.21
53	12503.85	nc	12971.14	12653.83	nc
56	11844.41	11865.66	14690.47	nc	nc
61	11774.26	11678.68	12651.47	12024.21	11586.98
62	12655.61	nc	nc	12808.44	12708.07
111	12004.30	15234.62	13005.50	12397.32	15260.52
119	12054.22	nc	nc	12204.67	12730.50
125	12193.33	nc	nc	nc	12806.82
136	11733.18	nc	nc	11942.21	12557.65

A.8. East-central Illinois, rut

Deer no.	single	double	sw	swcovar	covar
5	12483.80	14499.30	15111.51	12706.85	14794.70
14	12243.70	12121.02	nc	12618.75	nc
15	13134.17	nc	12575.85	nc	nc
17	12383.85	nc	nc	13031.18	13413.50
25	10464.63	nc	nc	17964.50	13291.90
36	11994.26	13516.12	nc	nc	nc
47	12094.38	12243.36	11918.27	nc	nc
48	11954.01	13078.78	nc	nc	nc
49	9632.13	26303.68	nc	nc	nc
52	12023.65	24071.13	nc	nc	34855.52
53	12554.46	12595.81	13266.55	13100.54	nc
56	12243.98	nc	nc	nc	nc
61	12174.52	nc	nc	nc	nc
62	12824.01	13611.51	14066.84	13457.22	13462.16
111	12524.58	13240.13	nc	12751.56	13713.79
119	12642.98	nc	nc	13211.75	19975.95
125	11884.39	13005.96	12272.40	12054.85	15851.71
136	12254.37	nc	nc	12436.05	17242.65

APPENDIX B

Average means of the posterior distribution of movement model parameters for the southern Illinois and east-central Illinois study sites, by season. Standard deviation (among animals) is in parenthesis. *n* depicts the number of animals that obtained convergence.

B.1. Single model.

Parameters	Gestation	Fawning	Prerut	Rut
southern Illinois				
n	27	20	19	25
a	6.590(1.550)	6.919(1.866)	5.582(1.640)	6.026(1.377)
b	0.870(0.200)	0.895(0.185)	0.888(0.101)	0.823(0.133)
μ	0.305(1.614)	3.870(1.787)	1.830(1.744)	1.833(1.279)
ρ	0.051(0.037)	0.071(0.034)	0.087(0.051)	0.075(0.039)
east-central Illinois				
n	20	19	18	18
a	4.166(0.949)	4.899(1.362)	4.841(1.257)	4.918(1.868)
b	0.779(0.169)	0.828(0.148)	0.801(0.116)	0.808(0.173)
μ	2.387(1.739)	2.764(1.150)	2.566(0.822)	2.741(0.527)
ρ	0.049(0.034)	0.080(0.047)	0.090(0.057)	0.095(0.045)

B.2. Double model

Parameters	Gestation	Fawning	Prerut	Rut
southern Illinois				
n	18	15	14	9
a_1	70.802(81.392)	28.511(17.664)	25.781(24.058)	46.652(33.200)
a_2	6.067(1.880)	6.830(2.658)	6.338(4.472)	5.005(2.632)

B. 2. Continued

Parameters	Gestation	Fawning	Prerut	Rut
b_1	1.256(0.150)	1.187(0.095)	1.171(0.207)	1.345(0.466)
b_2	1.359(0.167)	1.166(0.200)	1.271(0.272)	1.067(0.209)
μ_1	5.428(1.570)	0.414(0.984)	1.000(1.392)	2.657(1.350)
μ_2	0.256(0.668)	5.435(1.609)	0.084(0.787)	0.152(0.772)
ρ_1	0.100(0.077)	0.093(0.038)	0.131(0.070)	0.198(0.055)
ρ_2	0.068(0.050)	0.128(0.059)	0.146(0.117)	0.093(0.052)
η_{1t}	0.601(0.003)	0.578(0.003)	0.444(0.007)	0.418(0.007)
east-central Illinois				
N	16	10	7	10
a_1	20.880(7.613)	13.560(9.480)	31.627(26.662)	18.259(13.376)
a_2	3.945(1.158)	4.676(1.455)	5.902(1.572)	4.812(1.919)
b_1	1.089(0.097)	1.022(0.250)	1.102(0.148)	1.060(0.144)
b_2	1.159(0.176)	1.020(0.213)	1.226(0.277)	1.095(0.241)
μ_1	2.672(0.668)	0.912(1.556)	2.879(2.042)	2.000(1.237)
μ_2	0.355(0.656)	2.774(1.363)	0.893(1.140)	1.454(1.145)
ρ_1	0.108(0.041)	0.171(0.139)	0.149(0.061)	0.156(0.051)
ρ_2	0.063(0.038)	0.181(0.072)	0.117(0.056)	0.126(0.119)
η_{1t}	0.517(0.006)	0.531(0.009)	0.496(0.002)	0.423(0.008)

B.3. Switch model.

Parameters	Gestation	Fawning	Prerut	Rut
southern Illinois				
n	11	8	9	7
a_1	61.961(28.322)	27.657(18.437)	21.754(14.537)	22.674(28.251)
a_2	5.081(0.620)	5.854(2.260)	5.359(5.446)	4.290(4.346)
b_1	1.385(0.346)	1.162(0.155)	1.225(0.334)	1.279(0.364)
b_2	1.086(0.112)	1.155(0.307)	2.392(2.609)	1.338(0.477)
μ_1	5.099(1.824)	5.851(1.116)	0.550(1.055)	1.773(0.977)
μ_2	6.272(0.756)	6.157(1.298)	0.522(0.770)	0.534(0.714)
$q_{1,2}$	0.450(0.196)	0.834(0.135)	0.652(0.198)	0.751(0.229)
$q_{2,1}$	0.226(0.110)	0.216(0.157)	0.425(0.159)	0.345(0.129)

B.3. Continued

Parameters	Gestation	Fawning	Prerut	Rut
ρ_1	0.159(0.078)	0.093(0.044)	0.106(0.056)	0.144(0.081)
ρ_2	0.084(0.063)	0.097(0.047)	0.218(0.132)	0.185(0.147)
east-central Illinois				
n	10	6	7	6
a_1	57.685(46.166)	23.806(12.173)	32.026(31.358)	24.620(19.261)
a_2	3.676(1.466)	2.903(1.223)	5.049(2.950)	2.736(0.995)
b_1	1.250(0.214)	1.136(0.077)	1.482(0.504)	1.049(0.061)
b_2	1.224(0.224)	1.336(0.602)	1.323(1.066)	1.469(1.200)
μ_1	2.594(0.675)	3.059(0.100)	2.662(0.824)	2.706(0.215)
μ_2	0.605(0.920)	0.344(0.993)	1.612(1.253)	0.847(0.700)
$q_{1,2}$	0.753(0.243)	0.702(0.176)	0.590(0.209)	0.740(0.272)
$q_{2,1}$	0.238(0.182)	0.331(0.102)	0.287(0.116)	0.369(0.105)
ρ_1	0.113(0.066)	0.151(0.040)	0.187(0.059)	0.112(0.037)
ρ_2	0.119(0.183)	0.099(0.076)	0.118(0.099)	0.213(0.196)

B.4. Switch with covariates model.

Parameter	Gestation	Fawning	Prerut	Rut
southern Illinois				
n	21	14	15	14
a_1	93.349(86.757)	25.04(20.57)	27.381(33.146)	61.157(40.281)
a_2	6.784(2.216)	6.242(1.828)	6.257(3.303)	5.933(1.919)
b_1	1.316(0.153)	1.138(0.111)	1.064(0.119)	1.193(0.104)
b_2	1.318(0.202)	1.083(0.205)	1.248(0.353)	1.256(0.338)
μ_1	5.307(2.051)	5.895(0.892)	0.391(1.224)	2.639(1.995)
μ_2	6.214(0.524)	6.100(0.920)	0.245(1.081)	0.053(0.457)
ρ_1	0.19(0.243)	0.105(0.056)	0.14(0.081)	0.188(0.052)
ρ_2	0.077(0.05)	0.129(0.069)	0.167(0.122)	0.095(0.075)
β_1	0.191(0.187)	0.159(0.169)	0.104(0.108)	0.286(0.161)
β_2	-0.613(1.038)	-0.158(0.169)	-0.116(0.126)	-0.361(0.208)
$m_{2,1}$	0.551(0.14)	0.688(0.181)	0.745(0.111)	0.595(0.131)
$m_{2,2}$	0.408(0.333)	0.495(0.292)	0.468(0.306)	0.253(0.184)
$m_{2,3}$	0.229(0.246)	0.516(0.301)	0.458(0.292)	0.174(0.177)

B.4. Continued

Parameter	Gestation	Fawning	Prerut	Rut
$m_{2,4}$	0.216(0.304)	0.331(0.304)	0.386(0.322)	0.109(0.132)
$m_{2,5}$	0.226(0.282)	0.404(0.307)	0.455(0.344)	0.132(0.151)
$m_{2,6}$	0.255(0.242)	0.48(0.252)	0.448(0.255)	0.196(0.152)
$m_{2,7}$	0.42(0.412)	0.491(0.291)	0.506(0.273)	0.284(0.267)
$m_{2,8}$	0.232(0.22)	0.427(0.284)	0.449(0.271)	0.213(0.2)
$m_{2,9}$	0.38(0.362)	0.477(0.336)	0.626(0.468)	0.222(0.22)
east-central Illinois				
n	13	5	10	10
a_1	4.539(1.052)	6.125(2.728)	4.659(1.326)	5.882(2.936)
a_2	4.052(0.824)	4.134(0.869)	3.97(1.087)	4.996(2.433)
b_1	0.834(0.045)	0.936(0.098)	0.798(0.102)	0.812(0.181)
b_2	0.824(0.048)	0.857(0.043)	0.775(0.091)	0.857(0.177)
μ_1	1.116(1.107)	4.743(2.066)	1.057(0.662)	1.084(1.030)
μ_2	1.310(1.152)	0.151(0.707)	1.325(0.976)	0.712(1.019)
ρ_1	0.093(0.064)	0.103(0.068)	0.104(0.06)	0.115(0.016)
ρ_2	0.182(0.094)	0.175(0.094)	0.203(0.117)	0.19(0.043)
β_1	0.017(0.01)	0.013(0.036)	0.01(0.011)	0.012(0.014)
β_2	-0.01(0.018)	-0.014(0.031)	0.003(0.007)	-0.003(0.004)
$m_{2,1}$	0.799(0.01)	0.777(0.041)	0.795(0.007)	0.794(0.009)
$m_{2,2}$	0.785(0.049)	0.728(0.161)	0.795(0.007)	0.792(0.016)
$m_{2,3}$	0.761(0.102)	0.77(0.049)	0.8(0.01)	0.779(0.043)
$m_{2,4}$	0.748(0.159)	0.658(0.288)	0.793(0.014)	0.773(0.031)
$m_{2,5}$	0.79(0.032)	0.726(0.156)	0.801(0.014)	0.786(0.018)
$m_{2,6}$	0.799(0.025)	0.738(0.142)	0.793(0.009)	0.786(0.027)
$m_{2,7}$	0.802(0.028)	0.724(0.169)	0.796(0.009)	0.794(0.012)
$m_{2,8}$	0.751(0.159)	0.716(0.178)	0.799(0.013)	0.766(0.055)
$m_{2,9}$	0.776(0.057)	0.743(0.121)	0.797(0.01)	0.779(0.04)
$m_{2,10}$	0.766(0.074)	0.645(0.323)	0.794(0.013)	0.785(0.02)
$m_{2,11}$	0.749(0.149)	0.787(0.005)	0.792(0.01)	0.789(0.008)
$m_{2,12}$	0.729(0.192)	0.635(0.324)	0.787(0.015)	0.772(0.053)
$m_{2,13}$	0.707(0.204)	0.662(0.293)	0.796(0.012)	0.786(0.028)

B.5. Double with covariates model.

Parameters	Gestation	Fawning	Prerut	Rut
southern Illinois				
n	11	12	11	7
a_1	29.138(21.16)	29.976(19.954)	31.908(26.732)	43.556(23.613)
a_2	5.917(1.603)	6.618(2.939)	7.246(5.145)	5.532(1.51)
b_1	1.16(0.142)	1.161(0.094)	1.13(0.109)	1.19(0.082)
b_2	1.348(0.296)	1.206(0.244)	1.365(0.326)	1.231(0.095)
μ_1	6.184(1.100)	0.168(1.597)	1.580(1.496)	0.851(1.568)
μ_2	0.185(0.791)	5.523(1.508)	0.268(1.031)	0.010(0.297)
ρ_1	0.082(0.076)	0.093(0.035)	0.138(0.082)	0.25(0.245)
ρ_2	0.084(0.088)	0.11(0.054)	0.116(0.085)	0.084(0.062)
v_1	1.323(0.605)	1.574(1.253)	0.779(0.256)	1.332(0.609)
v_2	0.589(0.242)	1.301(1.387)	0.81(0.142)	0.588(0.112)
v_3	0.58(0.289)	0.596(0.204)	0.78(0.035)	0.55(0.163)
v_4	0.768(0.115)	1.034(0.8)	0.932(0.234)	0.808(0.091)
v_5	0.79(0.054)	0.824(0.139)	0.804(0.05)	0.762(0.042)
v_6	0.803(0.075)	0.814(0.062)	0.787(0.054)	0.769(0.048)
v_7	0.79(0.048)	0.767(0.054)	0.804(0.037)	0.771(0.041)
v_8	0.765(0.067)	0.78(0.119)	0.782(0.092)	0.839(0.19)
v_9	0.698(0.186)	0.725(0.248)	0.762(0.102)	0.75(0.252)
east-central Illinois				
n	9	7	12	9
a_1	17.026(8.558)	20.388(7.624)	24.722(13.822)	14.831(6.541)
a_2	3.382(1.314)	4.053(1.137)	5.066(1.729)	4.088(1.683)
b_1	1.068(0.114)	1.165(0.053)	1.018(0.09)	0.963(0.07)
b_2	1.336(0.23)	1.091(0.202)	1.429(0.192)	1.101(0.168)
μ_1	2.246(1.389)	4.846(1.250)	2.534(1.075)	1.305(1.752)
μ_2	0.329(0.672)	1.271(2.123)	1.081(1.073)	1.398(1.429)
ρ_1	0.795(0.008)	0.796(0.01)	0.792(0.005)	0.795(0.007)
ρ_2	0.786(0.031)	0.797(0.011)	0.792(0.021)	0.8(0.016)
v_1	0.085(0.044)	0.087(0.032)	0.106(0.036)	0.104(0.031)
v_2	0.067(0.03)	0.161(0.081)	0.11(0.082)	0.129(0.076)
v_3	3.139(1.787)	3.064(1.534)	1.51(0.909)	1.219(0.71)
v_4	0.807(0.154)	0.646(0.141)	0.904(0.453)	0.784(0.124)
v_5	0.38(0.251)	0.443(0.193)	0.606(0.693)	0.512(0.16)
v_6	0.768(0.044)	0.83(0.104)	0.815(0.069)	0.788(0.023)
v_7	0.775(0.091)	0.796(0.047)	0.740(0.129)	0.795(0.082)
v_8	0.801(0.014)	0.796(0.007)	0.802(0.01)	0.798(0.01)
v_9	0.752(0.027)	0.787(0.046)	0.771(0.031)	0.767(0.036)

B.5. Continued.

Parameters	Gestation	Fawning	Prerut	Rut
v_{10}	0.768(0.049)	0.769(0.057)	0.789(0.026)	0.784(0.021)
v_{11}	0.732(0.055)	0.751(0.045)	0.72(0.081)	0.748(0.069)
v_{12}	0.783(0.015)	0.79(0.029)	0.799(0.027)	0.811(0.032)
v_{13}	0.729(0.08)	0.763(0.157)	0.796(0.129)	0.765(0.061)

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