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Charles W. Anderson

Southern Illinois University Carbondale

Clayton K. Nielsen

Southern Illinois University Carbondale

Eric M. Schauber

Southern Illinois University Carbondale, schauber@siu.edu

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ORIGINAL ARTICLE

SURVIVAL AND DISPERSAL OF WHITE-TAILED DEER IN THE AGRICULTURAL LANDSCAPE OF EAST-CENTRAL ILLINOIS

C. W. Anderson^{1,*}, C. K. Nielsen² & E. M. Schauber³

¹ Cooperative Wildlife Research Laboratory, 251 Life Science II, Southern Illinois University Carbondale, Carbondale, IL 62901-6504, USA, Tel: (618) 536-7766; Fax: (618) 453-6944.

² Cooperative Wildlife Research Laboratory, Department of Forestry, and the Center for Ecology, 251 Life Science II, Southern Illinois University Carbondale, Carbondale, IL 62901-6504, USA, Tel: (618) 536-7766; Fax: (618) 453-6944, e-mail: kezo92@siu.edu.

³ Cooperative Wildlife Research Laboratory, Department of Zoology, and the Center for Ecology, 251 Life Science II, Southern Illinois University Carbondale, Carbondale, IL 62901-6504, USA, Tel: (618) 536-7766; Fax: (618) 453-6944, e-mail: schauber@siu.edu

* Corresponding author email: anderson.w.charles@gmail.com.

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White-tailed deer.

Abstract

White-tailed deer (*Odocoileus virginianus*) are a keystone species throughout their range in North America. The recent presence of diseases such as chronic wasting disease and bovine tuberculosis in Midwestern North America dictates the examination of influences of those diseases on deer populations, and survival and dispersal rates are important parameters when modeling potential disease spread. We quantified survival and dispersal rates of 105 deer in agriculturally-dominated east-central Illinois during 2005-2009. We used Program MARK to estimate rates of annual survival, seasonal survival, and dispersal for fawn, yearling, and adult age-classes. Male and female seasonal (winter/spring [16 Dec–14 May], summer [15 May–30 Sep], and fall/winter [1 Oct–15 Dec]) survival ranged from 0.56-0.95 and 0.84-0.96, respectively. Male survival was lower than female survival during the fall/winter season. Dispersal rates for yearling and fawn males and yearling and fawn females were 0.44 ± 0.07 and 0.41 ± 0.07 , respectively. The dispersal rate of adult males was 0.46 ± 0.15 and no adult females dispersed. Deer survival appears to be higher than previously reported in the region, with important implications for potential disease spread. Furthermore, the observation of long-distance dispersal (42–96 km) combined with greater estimates of survival may impact current chronic wasting disease modeling efforts.

Introduction

White-tailed deer (*Odocoileus virginianus*) are an ecologically, economically, and socially important species throughout their range in North America. Due to the value of white-tailed deer to numerous stakeholders (i.e., hunting and nonhunting public, state

and federal agencies), quantification of demographic aspects of deer populations such as survival and dispersal is a continual focus of research. Survival rates of white-tailed deer in agriculturally-dominated Illinois, USA, and other Midwestern states vary due to landscape (e.g., composition of forest cover, road density) and deer harvest levels. White-tailed deer harvest in Illinois has increased steadily since 1957 with hunting as the primary source of deer mortality in the state [1]. Nixon et al. [2] reported annual survival rates in east-central Illinois of adult males and females and yearling males and females as 0.39, 0.71, 0.38, and 0.62, respectively. Annual survival for adult males in northern Illinois was estimated to be 0.39–0.56 [3]. Brinkman et al. [4] estimated annual adult female survival rate of 0.77 in southwestern Minnesota. Differences in survival rates within the region vary largely due to differences in harvest regimes, predator influences, and climate.

Dispersal rates and distances in white-tailed deer are often influenced by landscape context, social pressures and sex/age of individuals. For male white-tailed deer, dispersal rates and distances decreased with greater amounts of forest land cover and increased with greater fragmentation [2, 5, 6]. Deer dispersal generally occurs during family breakup, late spring and in early fall [3], and is often caused by social pressures in the population [7]. Population density does not appear to influence dispersal rate or distance in white-tailed deer [2, 5, 6]. On average, 50% of male and female fawns disperse in east-central Illinois [2], but rates range from 0.39 to 0.65 [8]. Males maintain a similar dispersal rate from fawn to yearling age classes, but dispersal rates typically decrease with maturity [3, 9]. Skuldt et al. [6] reported a dispersal rate for yearling males of 0.45 in Wisconsin, but only <0.01 (1 of 108) for yearling females. In contrast, about 20% of yearling females dispersed in agriculture-dominated central Illinois [2]. Natal philopatry of females is associated with the matrilineal system of white-tailed deer [10, 11].

Accurate and current estimates of age-specific survival and dispersal are crucial for managing deer populations, particularly in the context of zoonotic disease and emerging diseases such as chronic wasting disease (CWD) and bovine tuberculosis (BT). Projecting population abundance and age structure under harvest and other management actions requires reliable age-specific survival rates, and background survival rates also influence the potential establishment and spread of disease. Both CWD and BT are characterized by infectious periods lasting months to years [12, 13, 14, 15], so lower background survival rates imply less time for infectious individuals to transmit to others, thereby reducing the basic reproductive number (R_0) of disease [16]. Improved information on dispersal rates can also inform management, because dispersal is a primary mechanism of patch colonization and gene flow, and as well as the geographic spread of pathogens.

The goal of our study was to quantify sex, age, and season-specific survival and dispersal rates of white-tailed deer in east-central Illinois, USA, and document causes of mortality. Updates to >20-year-old estimates of survival and dispersal rates of deer in east-central Illinois are needed since Illinois conducts active CWD management and given newly discovered locations of CWD-positive deer in neighboring Midwestern states [e.g., Missouri, Iowa; 17]. Furthermore, given recent concerns about potential deer declines in east-central Illinois unrelated to CWD [18], wildlife biologists in Illinois were seeking updated demographic information to set appropriate harvest levels.

Methods

Study area

We conducted field work on lands immediately surrounding the Lake Shelbyville Project (LSP; 13,892 ha; Fig. 1) operated by the U.S. Army Corps of Engineers in Moultrie and Shelby counties, Illinois, USA. Within the Lake Shelbyville Project are Lake Shelbyville, Eagle Creek State Park, Wolf Creek State Park, and Lake Shelbyville Fish and Wildlife Management Area. The study area has limited topographical relief with the exception of the land immediately surrounding the LSP which is characterized by varying degrees of ravines and drainages feeding into the lake. The majority of land area surrounding the LSP is row-crop agriculture, primarily planted with corn (*Zea mays*) and soybeans (*Glycine max*). Land cover classes present include agriculture (e.g., row-crop, hay field; 45.0%), developed (e.g., parking lots, homesteads; 4.0%), field (e.g., fallow field, pasture; 18.0%), forest (18.0%), wetland (5.0%), and water (10.0%). Forest land cover was largely composed of deciduous species (e.g., *Quercus* spp.). Forest cover was located immediately surrounding Lake Shelbyville, along riparian areas, and in small patches (about 2-16 ha) interspersed among agriculture fields. Predator species of white-tailed deer, likely mostly of fawns [49], were bobcat (*Lynx rufus*) and coyote (*Canis latrans*). White-tailed deer density ranged from 14.4–18.1 deer/km² from 2007–2008 [65]. White-tailed deer within the region tend to select agricultural fields for forage and cover and are forced into fragmented woodlots and forest cover surrounding the LSP after crop harvest [2].

The median period between first and last frost-free days on the study area was 183 days [19]. Average annual temperature ranged from 20.1° C in spring and summer (Apr–Sep) to 3.9° C in fall and winter [Oct–Mar, 19]. Average annual rainfall was 100.1 cm and average annual snowfall was 54.4 cm [19].

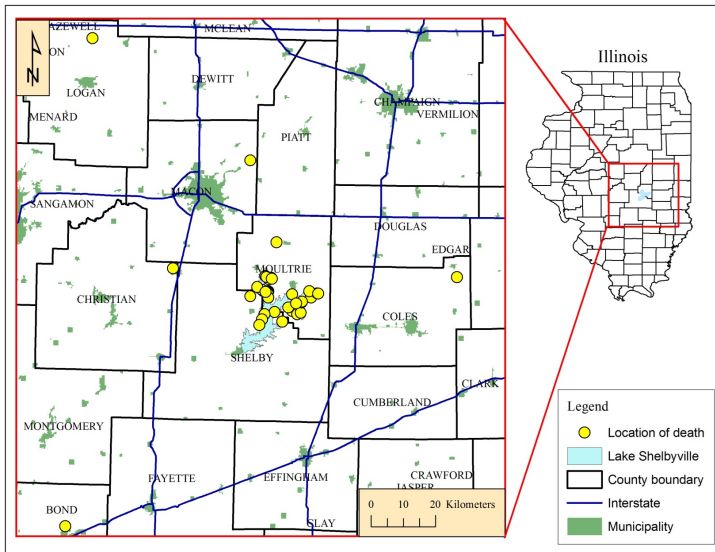


Fig. 1: Mortality locations of white-tailed deer (*Odocoileus virginianus*) captured on the Lake Shelbyville study area in east-central Illinois, USA, 2006–09. All captures occurred on lands immediately adjacent to Lake Shelbyville.

White-tailed Deer Capture and Marking

We captured white-tailed deer using tranquilizer darting (Pneu-dart Inc., Williamsport, Pennsylvania, USA), modified clover traps [20, 21], drop nets [22], and rocket nets [23]. We baited white-tailed deer to capture sites with corn and apples during the winters (Dec–Mar) of 2005–08. We immobilized captured white-tailed deer with an intramuscular injection (3cc) of a 2:1 mix of Telazol (Tiletamine HCl, 2 mg/kg and Zolazepam HCl, 4 mg/kg; Fort Dodge Laboratories, Inc., Fort Dodge, Iowa, USA) and Xylazine (Xylazine HCl, 2 mg/kg; Mobay Corporation, Shawnee, Kansas, USA) for darting [24] and a 9:1 mix of Ketaset (Ketamine HCL, 10 mg/kg, Fort Dodge Laboratories, Inc., Fort Dodge, Iowa, USA) and Xylazine for all other methods. We marked captured white-tailed deer with uniquely numbered ear tags; ears were disinfected with iodine prior to and after attachment. Captured white-tailed deer received either a VHF ear-tag transmitter (Advanced Telemetry Systems, Inc., Isanti, Minnesota, USA; 13 g; males and fawns), Global Positioning System (GPS) collar (Telonics, Inc., Mesa Arizona, USA; 700 g; adult and yearling females) or VHF radiocollar (Advanced Telemetry Systems, Inc., Isanti, Minnesota, USA; 500 g; adult and yearling females). We determined age via the tooth wear and development method [25]. We assessed capture myopathy by monitoring white-tailed deer daily for 4 weeks after capture [26, 27]. Capture and handling procedures were approved by Southern Illinois University Carbondale's Institutional Animal Care and Use Committee (protocol 06-002).

Radiotelemetry

During January 2006 to September 2009, we located white-tailed deer radiomarked via VHF transmitters using a receiver; a handheld, 4-element Yagi antenna; and a compass [28]. We obtained locations from 0500 to 2300 h for VHF-marked individuals ≥ 3 times per week. It is well established that white-tailed deer are most active during crepuscular periods, thus, we focused location gathering during that time [66–68]. To obtain each location, we took ≥ 3 bearings with < 20 minutes between the first and last bearing. We entered radiotelemetry data into LOCATE III to estimate white-tailed deer locations [29]; mean estimated location error was 1.3 ± 0.02 ha (SE throughout).

Global positioning system (GPS) collars were programmed to take geographic coordinates (hereafter, referred to as locations) every 2 hours except during the fall/winter season (Oct–Dec), when locations were taken every hour. Global positioning system collars were equipped with VHF transmitters for mortality or detachment monitoring. Mortality signals on VHF transmitter were programmed to initiate after 6-hours with no movement. We located GPS collars and downloaded locations upon collar detachment from a white-tailed deer (ca. 1 year post attachment).

Survival

When not collecting locations, we monitored survival of radiomarked white-tailed deer at least once weekly. If unable to locate a white-tailed deer for 10 days, we searched for the animal using a Cessna 172 aircraft with 2 H-Adcock antennas mounted to the wing struts. When a mortality signal was detected via radio monitoring, we retrieved the carcass and performed a field investigation to determine the cause of mortality. We

classified mortalities into 4 categories: predator, hunter-related, deer-vehicle-accident (DVA), and unknown.

We used the known-fates model (Kaplan-Meier survival analysis [30] modified for staggered entry [31]) in Program MARK to estimate annual and seasonal survival rates for fawn (<12 months old), yearling (12-23 months old), and adult (≥ 24 months old) white-tailed deer organized by 2-week intervals [32]. Neonates (fawns <6-months old) were not captured or monitored during this study. Upon reaching 15 May, age classes of actively monitored white-tailed deer were adjusted to the next class. We right-censored survival data for analysis. We divided the year into 3 seasons similar to Nixon *et al.* [2]: summer (15 May–30 Sep), fall/winter season (1 Oct–15 Dec), and winter/spring season (16 Dec–14 May). For each season, we exponentiated 2-week survival rates by the number of 2-week intervals in the season to yield full-season survival rates; annual survival rates were calculated by multiplying full-season survival rates [32]. Standard errors for full season and annual survival rates were calculated using the delta method [33]. We constructed 8 *a priori* models for 6 groups (adult male, AM; yearling male, YM; fawn male, FM; adult female, AF; yearling female, YF; and fawn female, FF) across the 3 seasons (Table 1). Models were constructed based on natural division in sex and season. We used Akaike’s Information Criterion adjusted for small sample sizes (AIC_c) to rank and select models [34] and considered models $<2 \Delta AIC_c$ units from the top model to be equally parsimonious [34]. When multiple models with $<2 \Delta AIC_c$ occurred, we used the model-averaging feature in MARK across those models to estimate survival rates. We generated Akaike weights (ω_i) to determine the relative degree that each model was supported by the data [34]. Goodness-of-fit tests are unavailable for the known-fates model; therefore, we performed a sensitivity analysis of the variance inflation factor [\hat{c} , 35]. We adjusted \hat{c} in small increments (0.25) from 1 (no overdispersion) to 3 (extreme overdispersion), examining whether model rankings changed in MARK [35, 36]. We made post hoc comparisons ($\alpha = 0.05$) of 2-week-interval survival rates by season within groups using Program CONTRAST [37].

Table 1: *A priori* models used to estimate survival rates of white-tailed deer (*Odocoileus virginianus*) in east-central Illinois, USA, 2006–09.

Model	K^a	Description
S ₁	1	Survival is constant (null model)
S ₂	3	Survival varies by age (A = adult, F = fawn, Y = yearling)
S ₃	2	Survival varies by sex (F = female, M = male)
S ₄	6	Survival varies by age and sex
S ₅	3	Survival varies by season (summer, fall/winter, and winter/spring)
S ₆	9	Survival varies by season and age
S ₇	6	Survival varies by season and sex
S ₈	18	Survival varies by season and sex and age

^a No. of parameters estimated

^b (Winter/spring + summer) vs. fall/winter

Dispersal

We considered a white-tailed deer a disperser if it left its home range [38] and was not relocated again by radiotelemetry within that home range [39]. A home range was constructed using a minimum of 30 locations (no more than one location per day) after capture using a 95% fixed kernel estimator [38]. We used the known fates model in Program MARK to estimate dispersal rates for the entire study period organized by

2-week intervals, treating the dispersal event as if it were a mortality [36]. We right-censored data for analysis. We constructed 8 *a priori* models for 6 groups (AM, YM, FM, AF, YF, FF; Table 2). Models were constructed based on natural divisions in sex and age with additional pooled models based on published observation of dispersal dominated by the younger age classes [2]. We used methods similar to survival analysis in ranking and averaging models, calculating ω_i , and conducting sensitivity analyses of \hat{c} .

Table 2: *A priori* models used to estimate dispersal rates of white-tailed deer (*Odocoileus virginianus*) in east-central Illinois, USA, 2006–09.

Model	K^a	Description
D ₁	1	Dispersal is constant (null model)
D ₂	2	Dispersal varies by sex
D ₃	3	Dispersal varies by age
D ₄	6	Dispersal varies by age and sex
D ₅	5	Dispersal varies by age and sex, except equal for YF and FF
D ₆	5	Dispersal varies by sex and age, except equal for YM and FM
D ₇	4	Dispersal varies by sex and age; equal for YM and FM, equal for YF and FF
D ₈	3	Dispersal varies by sex for adults; equal for YM, FM, YF and FF.

^a No. of parameters estimated

Results

We monitored 105 white-tailed deer (58 M, 47 F; 22 adults, 30 yearlings, 53 fawns) for 35,478 radiodays ($\bar{X} \pm \text{SE} = 159 \pm 17.0$ days per deer) for survival and dispersal analysis. Eight animals (7%) lost transmitters during the study and 12 transmitters (11%) failed due to broken antennas or battery exhaustion.

Survival

Thirty-nine of 105 radiomarked white-tailed deer died during our study (Fig. 1); of these, 23 were males (12 adults, 9 yearlings, 2 fawns) and 16 were females (9 adults, 6 yearlings, 1 fawn). Five white-tailed deer died from unknown causes, 6 from DVA, 1 from predators (coyote, *Canis latrans*), and 27 were hunter-related (i.e., harvested or wounded by hunters). Of the 5 deer that died of unknown causes, 4 were found in Lake Shelbyville but drowning was not confirmed as the cause of death; and the other carcass was extensively scavenged. Hunters harvested white-tailed deer a mean straight-line distance of 15.1 ± 4.7 km and a median distance of 3.9 km from the point of capture. One adult female moved a straight-line distance of 8.1 km from its home range during the fawning season and died via DVA <1 month later. The top model (S_7 , incorporating differences among seasons and sexes) and the number of models with $\Delta\text{AIC}_c < 2$ did not change until $\hat{c} > 2.5$. Therefore, we present results for $\hat{c} = 1.0$ and $\hat{c} = 3.0$. With $\hat{c} > 1.0$, no other model had AIC_c within 10 units of S_7 , which had essentially all Akaike weight ($w_i = 1.0$). The top model for $1.0 < \hat{c} < 2.5$ (S_7) retained $\Delta\text{AIC}_c < 2$ and had the lowest deviance when $\hat{c} > 2.5$. Therefore, we made inferences based on $\hat{c} = 1.0$. Model S_7 , which incorporated survival differences among seasons and sexes, had 30.7 times more weight than the next model. Full season survival rates of males ranged from 0.56 to 0.95 across the three seasons, with an annual survival rate of 0.50 ± 0.27 (Table 3). We attribute the relatively large SE for the male annual survival rate to a low sample size in the adult male age class. Full season survival of

females ranged from 0.94 to 0.96 across the three seasons, with an annual survival rate of 0.85 ± 0.14 (Table 3). Estimates of 2-week survival rates for males were lower during fall/winter than the other two seasons, whereas estimates of 2-week survival rates for females were similar across seasons (Table 4). The fall/winter season was the only season in which 2-week survival differed between sexes, with males having a lower survival rate than females ($\chi^2 = 10.119$, $P = 0.002$).

Table 3: Estimated seasonal (winter/spring [16 Dec–14 May], summer [15 May–30 Sep], fall/winter [1 Oct–15 Dec]) survival rates (S) and associated sample sizes (n) and standard errors (SE) for each season from averaged top model sets for white-tailed deer (*Odocoileus virginianus*) in east-central Illinois, USA, 2006–09. Standard errors for full season were calculated using the delta method [33].

Season	Males					Females				
	2-week interval		Full season		n	2-week interval		Full season		n
	S	SE	S	SE		S	SE	S	SE	
Winter/spring	0.994	0.004	0.943	0.170	45	0.994	0.003	0.939	0.104	37
Summer	0.994	0.004	0.947	0.155	41	0.995	0.004	0.956	0.141	37
Fall/winter	0.890	0.030	0.558	0.485	29	0.988	0.007	0.941	0.184	28

Table 4: Chi-square (χ^2), degrees of freedom (df), and P -values of comparisons made between seasonal (winter/spring [16 Dec–14 May], summer [15 May–30 Sep], fall/winter [1 Oct–15 Dec]) 2-week-interval survival rates of white-tailed deer (*Odocoileus virginianus*) in east-central Illinois, USA, 2006–09.

Comparison	Male			Female		
	χ^2	df	P -value	χ^2	df	P -value
Overall	87.730	2	<0.001	0.795	2	0.672
Winter/spring vs summer	0.001	1	0.974	0.075	1	0.784
Summer vs fall/winter	11.820	1	<0.001	0.788	1	0.375
Fall/winter vs winter/spring	11.867	1	<0.001	0.577	1	0.448

Dispersal

Thirty-four of 105 white-tailed deer dispersed: 24 males (5 adults, 14 yearlings, 5 fawns) and 10 females (0 adults, 8 yearlings, 2 fawns). As expected, all dispersals occurred during late spring/early summer (May–June) and early fall (September–October). The top two dispersal models remained the only parsimonious models for all adjustments of \hat{c} , and there was no change in model rankings (Table 5); therefore, we made inferences based on $\hat{c} = 1.0$. The top two models were D_8 (equal rates for all yearlings and fawns) and D_7 (equal rates for yearlings and fawns by sex) with D_8 having 1.9 times more weight. Averaging across top models, dispersal rates for yearling + fawn males and yearling + fawn females were 0.44 ± 0.07 and 0.41 ± 0.07 , respectively. The dispersal rate for adult males was 0.46 ± 0.15 and no adult females dispersed. Known mortalities of dispersed white-tailed deer occurred an average straight-line distance of 23.7 ± 5.7 km from capture locations (median distance = 12.5 km). Long-distance dispersals were observed in five male fawns (42–95 km) and 1 female fawn (96 km, Figs. 1 and 2).

Table 5: Top dispersal models for white-tailed deer (*Odocoileus virginianus*) in east-central Illinois, USA, 2006–09. Abbreviations: AIC_c , Akaike’s Information Criterion adjusted for small sample size; ω_i , Akaike weight; K , n° of parameters estimated.

Model ^a	AIC_c	ΔAIC_c	ω_i	K	Deviance
D_8	281.6	0.0	0.47	3	86.0
D_7	282.9	1.3	0.25	4	85.2
D_6	284.2	2.5	0.13	5	84.5
D_5	284.9	3.2	0.09	5	85.2
D_4	286.2	4.5	0.05	6	84.5

^a Models are defined in Table 2

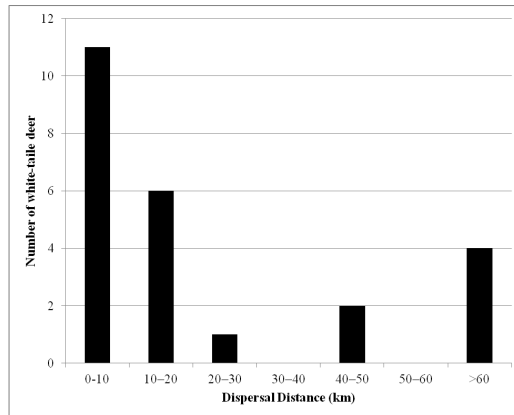


Fig. 2: Histogram of known dispersal distances of white-tailed deer (*Odocoileus virginianus*) in east-central Illinois, USA, 2006–09.

Discussion

Survival rates

We report annual survival rates for both male and female deer that are higher than previously reported in east-central Illinois and much of the Midwest region [2, Table 6]. Our estimates of female survival were higher than estimates in Nixon et al. [2] and other reports in the Midwest (Table 6), and male survival during fall/winter in our study was higher than survival of adult males documented by Nixon et al. [2] during a similar season. Because harvest was the primary mortality factor in our study area, hunter numbers or efficiency likely were relatively low in east-central Illinois during our study period. Moultrie and Shelby counties held a stable to increasing deer harvest from 2005–2010 with the overall number of deer hunting permits increasing across the state [40]. This is not fully indicative of hunter numbers given that hunters could purchase multiple permits, and it is likely that archery deer hunting has increased in popularity in Illinois. Although trends in total hunter numbers may be stable, this does not represent the potential for hunters merely switching their weapon of choice. Hunters using firearms are more efficient in harvest deer than with archery equipment [41]. Regardless of cause, annual survival during our study was higher than previously reported in the region.

The only sex-season effect on survival in our study was that survival of males was depressed during fall/winter, which is not surprising given that harvest (which occurs in that season and is biased toward males [42]) was the primary cause of mortality. As with Nixon et al. [2], the fall/winter season, which corresponds with most deer hunting seasons in the U.S., was the period with the lowest survival rates for males. Mortality due to DVA also may contribute to lower survival during fall/winter for deer as it is the peak time for DVA [43], which was observed in this study. Females had a greater 2-week-interval survival rate than males during fall/winter season, which is likely due to male bias in the hunter harvest [42].

Full-season survival rates for males and females during winter/spring were within ranges reported for both adult and yearling males in the Midwest (Table 6); conversely, rates in our study were higher than in the upper peninsula of Michigan

Table 6: Selected annual and seasonal survival rates of white-tailed deer (*Odocoileus virginianus*) by age and sex in the United States, 1986–2010.

Region	Citation	Sex	Age	Survival rate					
				Annual	January – May	June – September	October – December		
Exurban southern Illinois	[48]	Female	Adult	0.87	—	—	—		
Suburban Chicago, Illinois	[46]			0.83	0.92	0.96	0.93		
North-eastern Minnesota	[59]			0.79	—	—	—		
Southern Minnesota	[4]			0.77 ^a	0.95 ^b	1.00 ^c	0.80 ^d		
Upper Peninsula Michigan	[44]			0.77	0.89 ^e	0.90 ^f	0.96 ^g		
East-central Illinois	[2]			0.71	0.96	0.97	0.84		
North-central Minnesota	[45]			0.71	—	—	—		
Black Hills, South Dakota	[60]			0.57	—	—	—		
Suburban Chicago, Illinois	[46]			Female	Fawn	—	0.85	—	—
East-central Illinois	[2]					—	0.95	—	—
Upper Peninsula Michigan	[44]	—	0.68 ^e			—	—		
East-central Illinois	This study	0.85	0.94 ⁱ			0.96 ^j	0.94 ^k		
Upper Peninsula Michigan	[43]	0.89	0.93 ^a			1.00 ^f	0.95 ^g		
Suburban Chicago, Illinois	[46]	0.82	0.92			0.97	0.92		
North-eastern Minnesota	[59]	0.80	—			—	—		
East-central Illinois	[2]	0.62	0.97			0.85	0.67		
North-central Minnesota	[45]	0.60	—			—	—		
North-eastern Minnesota	[59]	Male	Adult			0.47	—	—	—
North-central Minnesota	[45]			0.44	—	—	—		
East-central Illinois	[2]			0.39	0.90	0.92	0.48		
Upper Peninsula Michigan	[44]			0.22	0.78 ^e	1.00 ^f	0.26 ^g		
Suburban Chicago, Illinois	[46]			—	0.93	1.00	0.89		
East-central Illinois	[2]			—	0.88	—	—		
Upper Peninsula Michigan	[44]			—	0.72 ^e	—	—		
East-central Illinois	This study			0.50	0.94 ⁱ	0.95 ^j	0.56 ^k		
North-central Minnesota	[45]			0.48	—	—	—		
East-central Illinois	[2]			0.38	0.63	0.94	0.58		
Upper Peninsula Michigan	[44]	Male	Fawn	0.25	1.00 ^e	0.83 ^f	0.32 ^g		
North-eastern Minnesota	[59]			0.41	—	—	—		
South-western Michigan	[61]			0.75 ^l	—	—	—		
South-central Iowa	[62]			0.73	—	—	—		
Southern Illinois	[49]			0.59	—	—	—		
North-eastern Minnesota	[59]			—	0.31	—	—		

^a Year 2001 only ^e 2 January–31 May ^l 16 December–14 May
^b January–April ^f 1 June–30 September ^j 15 May–30 September
^c May–August ^g 1 October–1 January ^k 1 October–15 December
^d September–December ^h Pooled age per best-fit modeling ^l Year 2002 only

where there is greater winter mortality [44; Table 6]. This is to be expected given the lower severity of winter and the lack of top carnivores in east-central Illinois. Summer survival of males was similar to estimates of male survival published previously by Nixon *et al.* [2] for a similar time frame (June–Sept) and within the ranges reported in the Midwest (Table 6). During summer, only studies from the upper peninsula of Michigan reported lower survival rates than our study; lower rates were for juveniles and attributed to predation [44, Table 6]. Full-season survival rates for adult females during summer were similar to rates of adult females reported by Nixon *et al.* [2]. Full-season survival rates for yearling females during summer were greater than reported by Nixon *et al.* [2]. Differences in yearling female survival are likely attributed to differences in limiting factors (e.g., deer density, habitat).

Causes of mortality

Causes of mortality in our study were similar to other Midwest deer studies, with hunting as the top mortality source for adult deer [4, 44, 45]. The percentage of deaths by DVA in our study was comparable to the percentage reported by Nixon *et al.* [1]

and within the range (5-23%) of other previous reports [2, 4]. In suburban and exurban landscapes with higher traffic volumes, DVA is often the top mortality source for deer [46, 47, 48]. Predators killed few white-tailed deer >6-months-old on our study area, as is generally true in areas free of top carnivores (e.g., cougar, *Puma concolor*; bear, *Ursus* spp.; [1, 2, 4]). We did not examine survival of neonates, but Nixon et al. [2] reported low predation rates on fawns (<6-months-old) in east-central Illinois. Other studies in agriculture-dominated regions of the Midwest [4, 6, 49] and elsewhere in North America [50, 51, 52], however, found predation to be the leading mortality source for young fawns [4, 6, 49].

Dispersal rates and distances

Dispersal rates of white-tailed deer are generally higher in agricultural landscapes relative to forested landscapes [7]. In our study, fawn dispersal rates were 14-22% lower than reported by Nixon et al. [2, 8]. However, the dispersal rate of yearling females was 51% greater than previously described by Nixon et al. [2] and may account for lower dispersal in the fawn class. Adult males had the highest dispersal rate in our study and at a higher rate than previously described in the Midwest (Table 7). These results, however, should be viewed with caution given the 2-year-old age class was included in this group and because of low sample size.

Table 7: Selected dispersal rates of white-tailed deer (*Odocoileus virginianus*) by age and sex in the United States, 1986–2010.

Region	Citation	Sex	Age	Dispersal rate
Eastern Nebraska	[63]	Female	Adult	0.30
Southern Illinois	[9]			0.07
Southern Minnesota	[64]			0.04
Southern Illinois	[11]			0.00
East-central Illinois	This study			0.00
East Illinois	[2]	Female	Fawn	0.50
Eastern Illinois	[8]			0.49
Northern Illinois	[8]			0.45
Western Illinois	[8]			0.22
Suburban Chicago, Illinois	[46]			0.07
Southern Minnesota	[64]			0.04
East-central Illinois	This study	Female	Fawn and yearling	0.41
East Illinois	[2]	Female	Yearling	0.21
Southern Illinois	[11]			0.13
Southern Illinois	[9]			0.13
Suburban Chicago, Illinois	[46]	Female	Yearling and adult	0.06
East-central Illinois	This study	Male	Adult	0.46
Southern Illinois	[9]			0.10
Southern Illinois	[11]			0.07
Western Illinois	[8]	Male	Fawn	0.78
Northern Illinois	[8]			0.68
Eastern Illinois	[8]			0.57
East Illinois	[2]			0.51
Suburban Chicago, Illinois	[46]			0.50
East-central Illinois	This study	Male	Fawn and yearling	0.44
Southern Illinois	[11]	Male	Yearling	0.80
Southern Illinois	[9]			0.80
Northern Illinois	[3]			0.75
Western Pennsylvania	[5]			0.74
Western Illinois	[3]			0.71
Eastern Illinois	[3]			0.55
Central Pennsylvania	[5]			0.46
Suburban Chicago, Illinois	[46]	Male	Yearling and adult	0.07
		Male		
Southern Illinois	[9]	and female	Fawn	0.04

Adult females did not disperse in our study, consistent with the findings of Nixon *et al.* [2] and other studies in the Midwest (Table 7). Adult females seem relatively philopatric regardless of habitat [2, 10, 44, 53]. Dispersal of female yearlings and fawns in our study were within the ranges previously reported for fawns in the Midwest, but higher than the range of yearling dispersal rates (Table 7). Etter *et al.* [54] reported that orphaning may increase female dispersal. Hunting was the main mortality source and increased harvest of females in the region relative to historical levels [40] may explain why yearling female dispersal rates were greater than previous reports (Table 7).

White-tailed deer in east-central Illinois have been documented dispersing >40–50 km but only ca. 25% of dispersers did so [10]. Average distance between capture and mortality locations of dispersers in our study was shorter than that reported by Nixon *et al.* [2], but was comparable to distances reported by Nixon *et al.* [10]. However, we documented 4 individuals that dispersed distances approaching 100 km, well beyond the average recorded by Nixon *et al.* [2]. Long-distance dispersals are more common in agricultural areas than forest-dominated regions [5, 7]. Nixon *et al.* [3] documented a male that dispersed 161 km, and Oyer *et al.* [55] reported a female that dispersed 98 km in agricultural landscapes. These long-distance dispersal events may be due in part to the lower amount of forest cover [7] combined with social pressures forcing deer to disperse [56]. Rare, long-distance dispersal events have disproportionate influence on the rates of population invasion, gene flow, and pathogen spread [57]. This landscape-dependent dispersal behavior of white-tailed deer may underlie the contrasting spatial distributions of CWD in largely forested south-central Wisconsin (compact and well defined) and the agriculture-dominated region on the Wisconsin-Illinois border (diffuse) [58]. Rather than posing a barrier, expanses of agricultural land are likely to accelerate movements of deer and their diseases by promoting long-distance dispersal.

Conclusions

Deer appear to be surviving at a higher rate than previously reported in east-central Illinois, which may have implications for models of population dynamics and disease spread. Higher survival rates within the region may indicate a greater number of deer available to potentially transmit a disease. Also, high baseline survival rates can increase the expected period when infectious hosts can transmit disease, thereby increasing opportunities for disease to establish and potential impacts on host populations. Hunting is the top mortality source in the region and for the state, thus management relies primarily on adjustments to hunting seasons or permit numbers. Our observations of long-distance dispersal movements suggest that dispersers could carry CWD or other diseases to distant populations. However, to fully examine influences on CWD dispersion, further work is needed to examine deer dispersal paths and how behavior and habitat may influence dispersal behavior in the agricultural Midwest.

There is a history of concern for white-tailed deer populations in east-central Illinois, such that low deer population numbers in 1999 led the Illinois Department of Natural Resources to restrict archery harvest in 5 counties in the region [Champaign, DeWitt,

Macon, Moultrie, and Piatt; 18]. However, the archery restriction has since been lifted, and hunting was the top mortality source for white-tailed deer in our study, as in much of the agricultural Midwest [2, 4]. Annual survival rates for both males and females were higher than previously reported in east-central Illinois [2], which may lend support to the cessation of archery restrictions for the region.

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Five “key references”, selected by the authors, are marked below (Three recommended (●) and two highly recommended (●●) papers).

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