

**NEONATAL SURVIVAL AND SPATIAL ECOLOGY OF ADULT FEMALE
WHITE-TAILED DEER IN THE FUNCTIONAL ABSENCE OF PREDATORS**

by

Justin R. Dion

A thesis submitted to the Faculty of the University of Delaware in partial fulfillment of the requirements for the degree of Master of Science in Wildlife Ecology

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ABSTRACT

White-tailed deer neonatal survival and adult female spatial behaviors are influenced by a wide array of variables. The emphasis on predator management as the driving factor in neonatal survival has distracted researchers from investigating other influential variables effecting survival, while female spatial behavior remains understudied in many systems. My overall objectives for this research were to (1) determine neonatal survival, (2) adult female spatial behavior, and (3) birth site selection in the absence of predators. I captured 52 adult females, followed by 109 neonates using opportunistic capture ($n = 55$) and vaginal implant transmitters (VIT; $n = 54$) in Sussex County, Delaware, USA during 2016 and 2017. Predators (i.e., black bear, bobcat, and coyotes) were functionally absent from the study area. The overall 90-day survival estimate was 0.54 (95% CI = 0.45 – 0.66). Opportunistically captured neonates had greater survival by 0.24, compared to VIT captured neonates ($z = 14.7$; $P < 0.01$). Natural causes ($n = 42$) accounted for all of my observed mortality. The top supported models included covariates for birth weight, doe maturity, and precipitation in the 7 and 30-day windows. Natural mortality is likely the ultimate mechanism controlling neonatal survival but is masked by the emphasis on predation and the inflated survival estimates caused by opportunistic capture.

Females decreased home range size following parturition with the smallest home ranges observed at 2 weeks post-parturition. Females who lost their fawns immediately increased their home range size back to pre-parturition sizes. Doe-to-fawn proximity decreased steadily, reaching its smallest distance at 4 weeks post-parturition. Mature females occupied smaller home ranges and remained closer to their

neonates for the first 5-6 weeks following parturition. The observed spatial behaviors fit well with trends in isolation behavior among females and timing of weaning for neonates.

In the absence of predators, females continued to select birth sites with superior predator avoidance cover. Females selected birth sites with 8% more horizontal cover than at paired-random sites. Canopy closure and basal area did not differ between observed and random sites, but this was likely due to the similarity in overstory composition and structure across large portions of the study area.

Chapter 1

NEONATE SURVIVAL IN THE FUNCTIONAL ABSENCE OF PREDATORS

To manage white-tailed deer (*Odocoileus virginianus*) populations, neonatal survival estimates must be incorporated into population models (Linnell et al. 1995, Chitwood et al. 2017). Studies in eastern North America over the past 20 years have documented neonatal survival estimates ranging from 87% in Minnesota (Grovenburg et al. 2011) to 14% in North Carolina (Chitwood et al. 2015; Table 1). Most of these survival studies list predation as the leading cause of mortality (Table 2). Although coyote (*Canis latrans*) are the most frequently documented predator, bobcat (*Lynx rufus*), black bear (*Ursus americanus*), and domestic dogs (*Canis lupus familiaris*) are other common predators (Table 3).

Table 1 Summary of white-tailed deer fawn survival studies from the eastern United States and Canada (1996-2017).

Citation	State/ Prov.	n	Capture Method ^c	60 Day Survival	90 Day Survival	Overall Survival
Ballard et al. 1999	NB	78	Opp.	-	0.47	0.23 ^a
Vreeland et al. 2004	PA	218	Opp.	0.65	-	0.53 ^b
Brinkman et al. 2004	MN	39	Opp.	-	0.84	0.84 ^a
Rohm et al. 2006	IL	166	Opp.	0.65	0.63	0.59
Burroughs et al. 2006	MI	75	Opp.	0.94	0.93	0.75
Saalfeld and Ditchkoff 2007	AL	36	VIT	0.33	-	0.33 ^b
Hiller et al. 2008	MI	34	Opp.	0.75	-	0.62 ^b
Grovenburg et al. 2011	MN	78	Both	0.95	-	0.87 ^b
Kilgo et al. 2012	SC	91	Both	-	-	0.22 ^{a b}
Grovenburg et al. 2012	SD	81	Opp.	-	0.74	0.74 ^a
Jackson and Ditchkoff 2013	AL	14	VIT	0.26	0.26	0.26
McCoy et al. 2013	SC	210	Opp.	-	-	0.67 ^{a b}
Duquette et al. 2014	MI	129	Both	-	-	0.19 ^{a b}
Chitwood et al. 2015	NC	65	Both	-	-	0.14
Shuman et al. 2017	LA	70	VIT		0.27	
Warbington et al. 2017	WI	228	Both	-	-	-
Northern Forest	-	89	-	-	-	0.45 ^{a b}
Eastern Farmland	-	139	-	-	-	0.65 ^{a b}

^a Unable to determine 60-day survival from data given.

^b Unable to determine 90-day survival from data given.

^c Opp. = Opportunistic

Table 2 Summary of cause-specific mortality from white-tailed deer fawn survival studies in the eastern United States and Canada (1996-2017). The top two most common mortality sources displayed along with the proportion of the total mortality each source comprised for each study.

Citation	Total Mortality ^a	Predation		Natural	
		n	%	n	%
Ballard et al. 1999	37	28	75%	-	-
Vreeland et al. 2004	106	49	46%	29	27%
Brinkman et al. 2004	6	4	67%	1	16.5%
Rohm et al. 2006	64	41	64%	5	7.8%
Burroughs et al. 2006	17	1	3%	5	29.4%
Saalfeld and Ditchkoff 2007	24	10	41.7%	8	33.3%
Hiller et al. 2008	10	3	30%	1	10%
Grovenburg et al. 2011	16	12	75%	3	18.8%
Kilgo et al. 2012	70	63	90%	10	14.3%
Grovenburg et al. 2012	23	12	52.2%	5	21.7%
Jackson and Ditchkoff 2013	9	7	77.8%	2	22.2%
McCoy et al. 2013	68	29	42.6%	22	32.4%
Duquette et al. 2014	65	49	75%	-	-
Chitwood et al. 2015	55	35	63.6%	19	34.6%
Shuman et al. 2017	51	45	88.2%	4	7.8%
Warbington et al. 2017	85	50	58.8%	23	27.1%

^a The number of deaths in each mortality category listed may not add up to the total number of mortality events for each study. Total mortality numbers include unknown causes and obscure causes that are not listed.

Table 3 Summary of mortalities attributed to specific mammalian predators in white-tailed deer fawn survival studies in the eastern United States and Canada (1996-2017). The top 4 most common predator species displayed along with the proportion of the total predation mortality each source comprised for each study.

Citation	Coyote		Bobcat		Black bear	
	n	%	n	%	n	%
Ballard et al. 1999	20	54.1%	2	4%	4	10%
Vreeland et al. 2004	28	57.1%	1	2%	8	16.3%
Penns Valley Site	5	62.5%	-	-	1	12.5%
Quehanna Wild Area	13	31.7%	3	7.3%	15	36.6%
Brinkman et al. 2004	2	50%	-	-	-	-
Rohm et al. 2006	23	56.1%	3	7.3%	-	-
Burroughs et al. 2006	1	100%	-	-	-	-
Saalfeld and Ditchkoff 2007	10	100%	-	-	-	-
Hiller et al. 2008	3	100%	-	-	-	-
Grovenburg et al. 2011	12	100%	-	-	-	-
Kilgo et al. 2012	56	88.9%	6	9%	-	-
Grovenburg et al. 2012	10	83.3%	-	-	-	-
Jackson and Ditchkoff 2013	6	66.7%	1	11.1%	-	-
McCoy et al. 2013	14	48.3%	7	24.1%	-	-
Duquette et al. 2014	23	47%	11	23%	4	8%
Chitwood et al. 2015	30	54.5%	5	9.1%	-	-
Shuman et al. 2017	9	20%	11	24.4%	17	37.8%
Warbington et al. 2017	24	48%	9	18%	10	20%

Whether predation on neonatal white-tailed deer is an ultimate or proximate cause of death is not well understood yet could change our perceptions of the impacts of predators on deer population dynamics. Determining the ultimate cause of mortality is inherently difficult in wildlife research because detailed animal condition data can typically only be collected at 2 times during the study: capture and mortality. The resulting data gap leaves researchers to speculate the chain of events leading up to the

mortality and determine cause of death based on the information available at the time of mortality (Chitwood et al. 2014, 2017).

Further complicating the issue is the inclusion of opportunistically captured animals in neonatal survival studies. Opportunistic capture relies on observing maternal behavior or searching fawning habitat to opportunistically capture fawns (Gilbert et al. 2014, Chitwood et al. 2017). Use of this method leads to biased survival estimates due to inaccurate age estimation and failure to observe mortalities occurring in the first days after birth (Ozoga and Rodney 1988, Haskell et al. 2007, Gilbert et al. 2014, Chitwood et al. 2017).

Predation as a cause of mortality is well documented, but other factors influencing survival have received less attention (Gingery et al. 2018). Several studies have documented that birth weight is positively correlated with survival probability in neonates (Linnell et al. 1995, Saalfeld and Ditchkoff 2007, McCoy et al. 2013). Additionally, a paucity of literature explores maternal influences and daily weather on neonate survival. Fawns of mature females may experience a lower risk of predation than those of younger females as a result of maternal experience and greater habitat quality (Ozoga and Verme 1986, Grovenburg et al. 2010). The influence of daily weather has been well documented in other species such as wild turkey (*Meleagris gallopavo*), where poult survival was negatively related to precipitation (Roberts and Porter 1998, Vangilder and Kurzejeski 1995). Precipitation presence and minimum temperature have been reported by some studies to influence neonatal survival at multiple spatial and temporal scales; however, results have been conflicting (Ginnett and Young 2000, Warbington et al. 2017, Michel et al. 2018). More research is needed

to better understand the influence of female age and weather variables on neonatal survival.

Natural mortality not related to predation (hereafter natural mortality) is less frequently observed than predation (Chitwood et al. 2017, Gingery et al. 2018). Examining neonatal survival in the functional absence of predators will provide information to wildlife biologist to better manage deer abundance. My objectives were to 1) estimate survival of white-tailed deer neonates in the absence of predators; 2) estimate apparent cause-specific mortality; 3) examine the influence of capture method (VIT vs. opportunistic) on survival estimates; and 4) assess how birth weight, doe maturity, and weather covariates influenced neonate survival.

Study Area

I conducted my research in Sussex County, Delaware (Figure 1). Bordering Sussex County is the Atlantic Ocean (east), Kent County, Delaware (north), and Maryland (south and west). Land use in the county was agriculture (41%), upland forest (22%), forested wetland (22%) and development (15%) (National Agricultural Statistical Service 2012). The major agricultural crops included corn, soybeans, and winter wheat (National Agricultural Statistical Service 2012).



Figure 1 Geographic reference for Sussex County, Delaware on the eastern coast of the USA. Sussex County represented by the shaded (dark grey) area.

Sussex County deer densities is approximately 19 deer/km² and has no established deer predator communities, aside from humans (Delaware Division of Fish and Wildlife 2010). Coyotes are rare in Sussex County; since the state opened a hunting and trapping season in 2014 only 9 have been harvested according to mandatory reporting data (Rogerson; unpublished data). No confirmed black bear or bobcat sightings have occurred in Sussex County for over 100 years. The only carnivores large enough to prey upon neonates were red fox (*Vulpes vulpes*).

Average annual precipitation during the study was 122 cm; similar to the 30-year (1981–2010) average of 119cm. Temperatures during the study (2015-2017) ranged from -14°C to 36°C (National Climatic Data Center 2012). Spring and Summer

precipitation averaged 78 cm, with temperatures ranging from 2°C to 36°C (National Climatic Data Center 2017).

Methods

Adult Capture

I captured adult females from December to April, 2015 – 2017 using rocket nets, drop nets, and clover traps baited with whole kernel corn (Schemnitz et al. 2012). Once captured, I blindfolded and physically restrained individuals, then chemically immobilized them using an intramuscular injection of xylazine (0.5mg/kg; Rhoads et al. 2013). I monitored vital rates at 5-minute intervals to ensure the health of each individual during the work up process. I marked each deer with unique numbered ear tags (one plastic and one metal in each ear). I estimated the age of each deer using tooth replacement and wear (Severinghaus 1949). I fit all females ≥ 1.5 years of age with collars and vaginal implant transmitters (VITs) from Advanced Telemetry Systems (Isanti, Minnesota). I deployed Neolink GPS collars (G2110E2 Iridium collars [800gr]) with VITs (M3930U [23gr]) on 44 females and standard VHF collar (M2230B [190gr]) with VITs (M3930 [21.5gr]) on an additional 8 females. I followed guidelines for VIT deployment established in Bowman and Jacobson (1998) and Carstensen et al. (2003). Following data collection, I administered an intramuscular injection of tolazoline (4mg/kg; Miller et al. 2004) to reverse the effects of the xylazine. I monitored animal condition and vitals, until recovery and individuals left the capture site under their own power. University of Delaware Institutional Animal Care and Use Committee approved all of my capture and handling procedures (#1288).

Predator Surveys

I monitored for presence of predators at each capture property using camera traps (Kelly and Holub 2008). I limited placement to ≤ 3 cameras (Reconyx© Hyperfire HC600; Holmen, Wisconsin) per site, depending on property size. I set camera traps over scent station which utilized predator baits and scent lures to increase the odds of capturing any predator or mesocarnivores in the area. I refreshed baits and scents every 2 weeks (Gompper et al. 2006, Kelly and Holub 2008). I also employed passive camera sets which were placed on high wildlife traffic areas (e.g.; field edges, game/hiking trails and travel corridors). In order to cover as much of the properties as possible, I placed cameras a minimum of 200 meters apart. I secured cameras 30 - 40 cm off the ground, allowing them to capture smaller mesocarnivores, such as raccoons (*Procyon lotor*) and red fox while still capturing larger animals (Kelly and Holub 2008). I conducted predator camera surveys from December to March during both the 2016 and 2017 seasons. I deployed 23 cameras across 12 adult and neonate capture properties, yielding a total of 9,379 photos over 1,186 trap nights. I observed no coyote, bobcat or black bear during my predator camera sampling. I recorded approximately 157 red fox sightings, as well as 6 unique domestic dog sightings. I also deployed camera traps on corn bait piles for the purpose of monitoring deer activity at various deer capture sites. I monitored deer activity from December to April during both my 2016 and 2017 seasons for a total of 2,735 trap nights. Though not intended to contribute to the predator survey, I captured a single photo of a coyote on 1 such deer camera trap site. I did not capture any further photos of the coyote at the site or any other camera sites in the area.

Adult and VIT Monitoring

I determined the location of VHF collared females and monitored VIT status weekly following deployment until 6 May. Starting 6 May, I increased the frequency of location fixes of VHF collared females and their VIT status monitoring to every six hours to timely notification of parturition (Saalfeld and Ditchkoff 2007, Kilgo et al. 2012, Jackson and Ditchkoff 2013). I received GPS locations and VIT status reports from the GPS collared females once per day, until 1 May. Following 1 May, I received GPS locations and VIT status reports once per hour. Once the collar recognized that the VIT had been expelled, I received an email notification.

Neonate Capture

Once the notification of VIT expulsion was received, I began searching for the fawns (1 – 2 hours after notification). I used the VHF signal emitted by the VIT to direct my search for the VIT and birth site. If the VIT was discovered outside of any apparent birth site, I marked the location of the VIT with flagging tape and searched the area until a birth site was found. Following the completion of the search for the birth site, I initiated the search for the neonates. If I did not locate the fawns in the immediate vicinity of the birth site, I systematically searched the surrounding area until one or more fawns were found. I used a thermal imaging camera (FLIR© Scout III 320; Wilsonville, Oregon) to aid in both day and nighttime searches (Saalfeld and Ditchkoff 2007, Kilgo et al. 2012, Jackson and Ditchkoff 2013). Throughout the season, I also opportunistically captured neonates that were found during daily activities and nocturnal searches. For nocturnal searches, I systematically searched fawning habitat using thermal scopes and spotlights to locate hiding neonates.

Once located, I blindfolded fawns and moved them to a work up location away from their individual bed sites to minimize human scent at bed sites. I wore non-scented latex gloves when handling the neonates to prevent human oils and scent from being transferred to the neonate during the work up (Kilgo et al. 2012). To measure capture/birth weight, I placed neonates in cotton pillowcases attached to a Pesola® Micro-line scale (10kg). Once weighed, I fit each neonate with an expandable VHF collar (M4210 [63gr], Advanced Telemetry Systems; Isanti; Minnesota) and marked them with uniquely numbered ear tags: one plastic and one metal in each ear. Once the work up was complete, I returned neonates to the bedsite at which they were captured and left the area as quickly as possible.

Neonate Survival Monitoring

I located neonates on an age-based schedule. For the first 30 days, I located individuals twice a day to ensure timely notification of mortality status during the period of greatest risk of mortality for neonates (Linnell et al. 1995, Saalfeld and Ditchkoff 2007). Between day 30 and 60, I located individuals once per day, then 3 times per week for 60-90 days. After 90 days, I located individuals once per week until the collar failed or a mortality occurred. When a mortality occurred, I tracked the signal to the carcass and examined the remains for an obvious cause of death (Cook et al. 1971, Linnell et al. 1995, Vreeland et al. 2004, Kilgo et al. 2012). If no obvious signs were observed and the viscera were intact (i.e.; limited scavenging), I collected the carcass and submitted it for gross necropsy and histology at the Pennsylvania Animal Diagnostic Laboratory (PADL) at The University of Pennsylvania.

Data Analysis

I estimated neonatal survival using a Kaplan-Meier survival function in program R using the package ‘survival’ at 30, 60, and 90 days post-parturition (Pollock et al. 1989). Using a log-rank test, I compared survival between sexes and years for all 3 survival windows (Wickham et al. 1993, Burroughs et al. 2006). If no difference was detected, I pooled data for sexes and years. Similarly, I compared survival estimates between capture methods (i.e.; opportunistic vs. VIT) using a log-rank test. I categorized mortalities as natural, predation, and unknown. Natural mortality included all natural causes of death other than predation (e.g.; emaciation, disease, stillborn). Predation mortality included all cases in which predators inflicted trauma that caused the death of an individuals. Unknown mortalities included all cases in which the specific cause of death could not be determined. I did not document any human induced mortalities such as from vehicle collisions or agricultural equipment. I determined cause of mortality by reviewing PADL necropsy and histology reports, discussing the reports with the veterinarians that conducted the necropsies, and notes and photographic observations from the field (Warbington et al. 2017).

I used Cox proportional hazard models (Cox 1972) to determine the impact of specific covariates on neonatal survival in the first 7 and 30 days of life (Duquette et al. 2014). I constructed 14 candidate models for each survival window which included covariates for birth weight, doe maturity, daily precipitation, and minimum temperature. I included birth weight because of the well documented influence on neonatal survival (Linnell et al. 1995, Saalfeld and Ditchkoff 2007, McCoy et al. 2013). I used doe maturity to explore the influence of both maternal experience and dominance on neonatal survival which has been reported in some observational studies (Ozoga and Verme 1986, Bertrand et al. 1996). I designated a female as mature if she

was > 4 years of age at the time of parturition. I used the 4-year requirements because females reach peak physical size around 3.5 years of age, making the following year their first full year as physiologically mature (Ditchkoff 2011). Additionally, after 4 years of age females have likely had 2 to 3 litters of fawns which makes them more experienced than younger females (Jones et al. 2010, Ditchkoff 2011). I included weather covariates for precipitation and minimum temperature, as these variables have been reported as potentially influencing neonatal survival (Ginnett and Young 2000, Warbington et al. 2017, Michel et al. 2018). I included only fawns captured using VITs because I were unable to link opportunistically captured fawns to their maternal doe or accurately estimate birth weight using capture weight and age. Using Akaike's Information Criterion (AICc) values, I compared my candidate models to identify influential covariates that explained the greatest amount of variation in neonate survival. Models with delta AIC values < 2 were designated as competing models (Hurvich et al. 1989, Klein and Moeschberger 1997).

Results

I captured 109 neonates using opportunistic capture (n = 55) and VITs (n = 54). Average birth date was 28 May, with the earliest birth occurring on 9 May and the latest occurring on 23 June. Between 18 May and 31 May, 67% of fawns were born. Sex ratio of capture neonates was 1:1 (female = 53; males = 56; Table 4). Average capture weight for all neonates was 3.96 kg (SE = 0.14 kg) and average birth weight for VIT fawns was 2.94 kg (SE = 0.06 kg). Average birth weight did not differ between fawns born from mature (\bar{x} = 2.96 kg, SE = 0.11) and immature (\bar{x} = 2.89 kg, SE = 0.07) females (t = -0.18; P = 0.86). Average age of opportunistically captured fawns was 6 days (range = 1 – 14 days; SE = 0.47).

Table 4 Sample size details for neonates captured in Sussex County, Delaware, USA (2016 and 2017). Including the number of neonates capture each year, by each capture method, and the sex ratio of the sample.

Year	n	Capture Method		Sex		Litter Size	
		VIT	Opportunistic	Male	Female	Singleton	Twin
2016	30	22	8	16	14	5	7
2017	79	32	47	40	39	3	11
Total	109	54	55	56	53	8	18

The 30-day survival estimate did not differ between years ($z = 1.5$; $P = 0.22$) or sex ($z = 0.2$; $P = 0.62$) and the combined survival rate for both years was 0.61 (95% CI = 0.51 – 0.72; Figure 2). The 30-day survival rate differed between capture methods ($z = 15$; $P < 0.01$). The opportunistically captured neonates (0.76, 95% CI = 0.61 – 0.94) had a 23% greater survival rate than VIT captured neonates (0.53, 95% CI = 0.41 – 0.68; Figure 3).

The 60-day survival estimate did not differ between years ($z = 2$; $P = 0.16$) or sex ($z = 0.7$; $P = 0.41$) and the combined survival rate for both years was 0.59 (95% CI = 0.50 – 0.71; Figure 2). The 60-day survival rate differed between capture methods ($z = 17.5$; $P < 0.01$). The opportunistically captured neonates (0.76, 95% CI = 0.61 – 0.94) had a 27% greater survival rate than VIT captured neonates (0.49, 95% CI = 0.37 – 0.65; Figure 3).

The 90-day survival estimate did not differ between years ($z = 0.6$; $P = 0.44$) or sex ($z = 0.7$; $P = 0.42$) and the combined survival rate for both years was 0.54 (95% CI = 0.45 – 0.66; Figure 2). The 90-day survival rate differed between capture methods ($z = 14.7$; $P < 0.01$). The opportunistically captured neonates (0.69, 95% CI = 0.55 – 0.87) had a 24% greater survival rate than VIT captured neonates (0.45, 95% CI = 0.34 – 0.61; Figure 3).

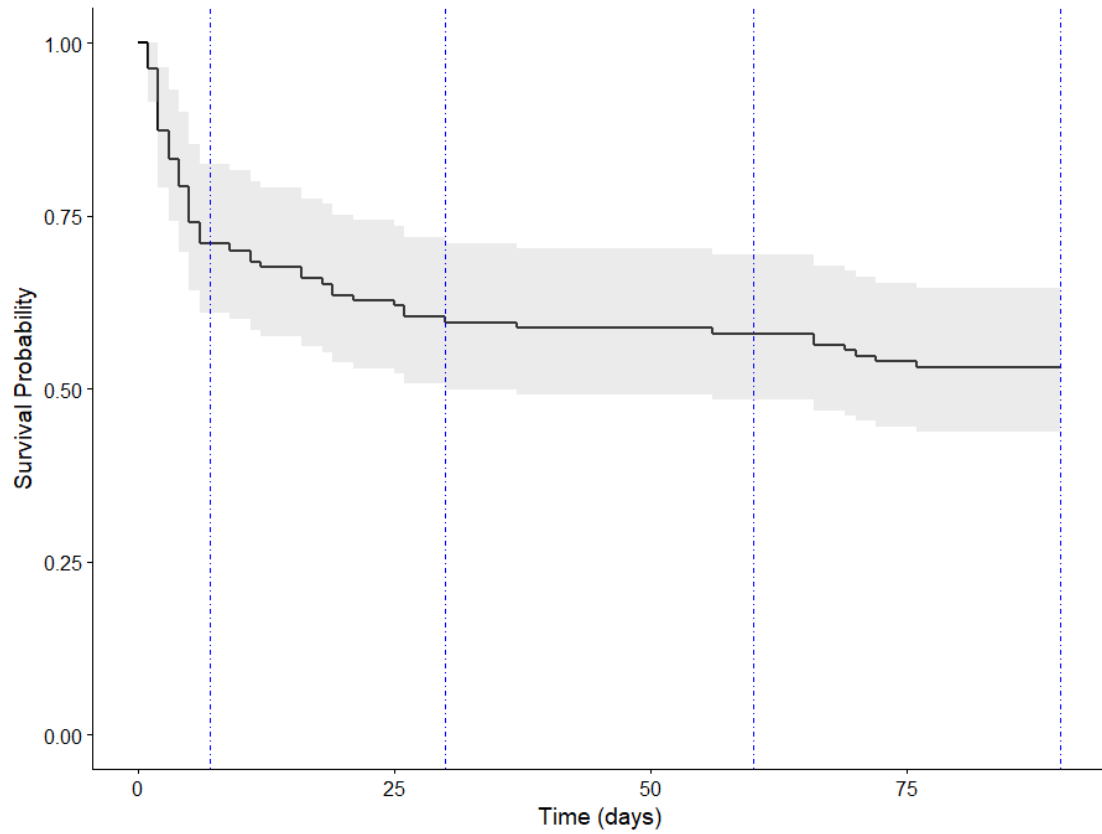


Figure 2 90-day Kaplan-Meier survival curve with 95% CI for neonates captured in Sussex County, Delaware, USA (2016 and 2017). All (n = 109) neonates included using staggered entry design to accommodate opportunistically captured individuals. For time reference, vertical lines represent 14, 30, 60, and 90-day marks.

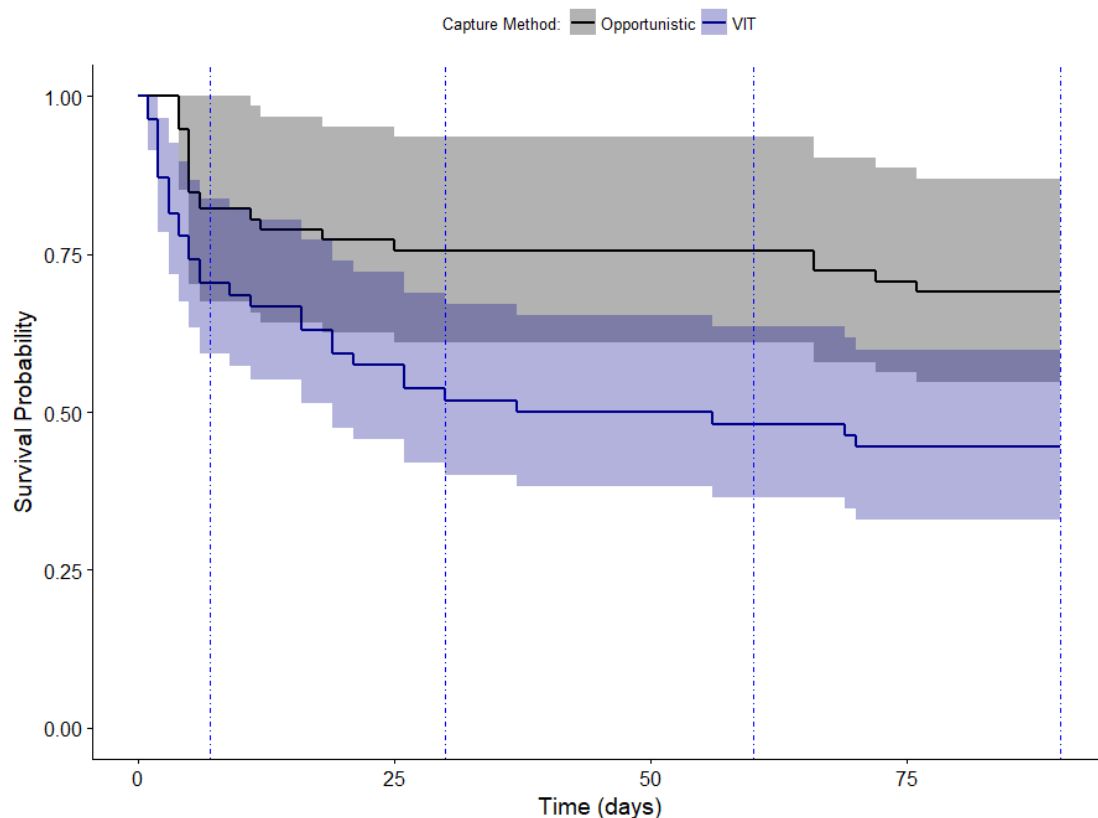


Figure 3 90-day Kaplan-Meier survival curve by capture method with 95% CI for neonates captured in Sussex County, Delaware, USA (2016 and 2017). For comparison, VIT (n = 54) and opportunistically (n = 55) captured neonates are graphed separately. For time reference, vertical lines represent 14, 30, 60, and 90-day marks.

I observed 42 mortalities within 90 days of birth; all of which were classified as natural mortality. Nearly half (47%; n = 20) of the mortalities occurred in the first 7 days of life and 81% (n = 34) occurred within 30 days of life. The leading cause of mortality was emaciation (50%; n = 21) for both opportunistic and VIT neonates. Of the observed emaciation, 62% (n = 13) had milk in the stomach at the time of death. Disease (21%; n = 9) was another substantial cause of natural mortality for neonates in

my study: bacterial infections (pleuropneumonia and sepsis, n = 7), ischemic hepatic necrosis (n = 1), and focal necrotizing encephalitis (n = 1). *Theileria cervi* was identified as the cause of death for 1 neonate but was present and may have contributed to mortality in 5 additional neonates. One mortality had signs of a possible red fox predation, based on canine size and separation. According to PADL pathologists, the neonate suffered a single canine puncture to the skull resulting in a subdural hemorrhage. The poor nutritional condition of the animal, along with the lack of subcutaneous bleeding suggested that the trauma was likely suffered at, or immediately prior to the time of death. The PADL pathologists stated that the fawn would have died without the bite wound; therefore, I classified this mortality as natural mortality resulting from emaciation. I observed 9 mortalities in which the cause of death could not be determined, of which the necropsy yielded no abnormalities for 2 and the remaining 7 were too heavily scavenged to submit for necropsy, although no signs of predation were apparent (Table 5).

Table 5 Proximate causes of mortality within 90 days of life for neonates captured in Sussex County, Delaware, USA (2016 and 2017). Proximate causes determined by field notes and Pennsylvania Animal Diagnostic Laboratory necropsy and histology reports. Secondary findings include contributing causes of mortality.

Proximal Cause	n	%	Secondary Findings			
			Heavy Ticks	<i>Theileria cervi</i> (Present)	Cranial trauma	Emaciation
Emaciation	21	50%	7	3	1	
Unknown	7	17%	2			
Bacterial Sepsis	4	10%				1
Bacterial Pleuropneumonia	3	7%	2	1		1
Unknown Natural	2	5%				
Ischemic Hepatic Necrosis	1	2%	1	1		
Focal Necrotizing Encephalitis	1	2%				
<i>Theileria cervi</i>	1	2%	1			1
Drowned	1	2%				
Unknown Trauma	1	2%				

Of my 14 candidate models (Table 6), I had 3 competing models for the 7-day window and 2 competing models for the 30-day window. For the 7-day window, my top competing models included birth weight, precipitation and doe maturity; explaining 80% of the variation in my survival data. Birth weight appeared in all 3 competing models. The univariate model for birth weight ($\beta = 0.10$; CI = 0.04 - 0.29) predicted for every 1 kg increase in a neonate's birth weight, its risk of mortality was reduced by 90% (Figure 4).

Table 6 Summary of AICc values generated by Cox proportional hazard 7-day survival models for neonates captured in Sussex County, Delaware, USA (2016 and 2017). Depicts the modelled influence of covariates on neonate survival in the first 7 days of life.

Model	AICc	Δ AIC	ω
Birth Weight + Precipitation	109.93	0.00	0.29
Birth Weight + Doe Maturity	110.13	0.20	0.26
Birth Weight	110.19	0.27	0.25
Birth Weight + Minimum Temperature	112.00	2.07	0.10
Birth Weight * Precipitation	113.01	3.08	0.06
Birth Weight * Minimum Temperature	114.35	4.42	0.03
Global	117.70	7.77	0.01
Precipitation	120.99	11.06	0.00
Doe Maturity	122.33	12.41	0.00
Null	122.70	12.78	0.00
Precipitation + Minimum Temperature	122.85	12.92	0.00
Minimum Temperature	124.22	14.29	0.00
Precipitation * Minimum Temperature	125.85	15.92	0.00
Birth Weight*Precipitation* Minimum Temperature	126.60	16.68	0.00

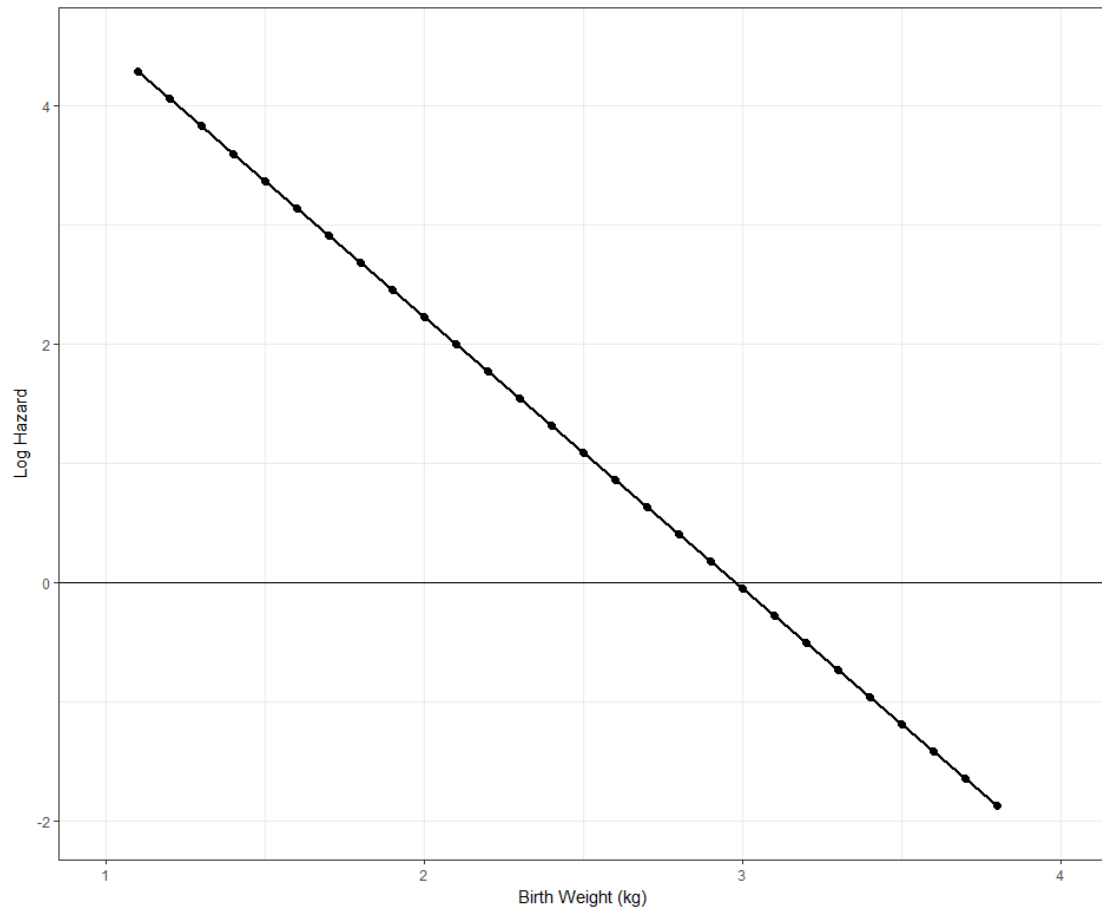


Figure 4 The influence of birth weight on the risk of mortality in the first 7 days of life for neonates captured in Sussex County, Delaware, USA (2016 and 2017). Log hazard (i.e.; β coefficient) graphed as the response variable to changes in covariate values.

The model including birth weight ($\beta = 0.12$; CI = 0.04 - 0.32) and precipitation ($\beta = 1.62$; CI = 1.08 – 2.43) predicted that at average birth weight (2.9) kg, every 1 cm increase in precipitation increased the instantaneous mortality risk by 62%. The effects of precipitation can be abated by an increase in birth weight, for every 1 kg increase in weight the instantaneous mortality risk decreased by 89% (Figure 5).

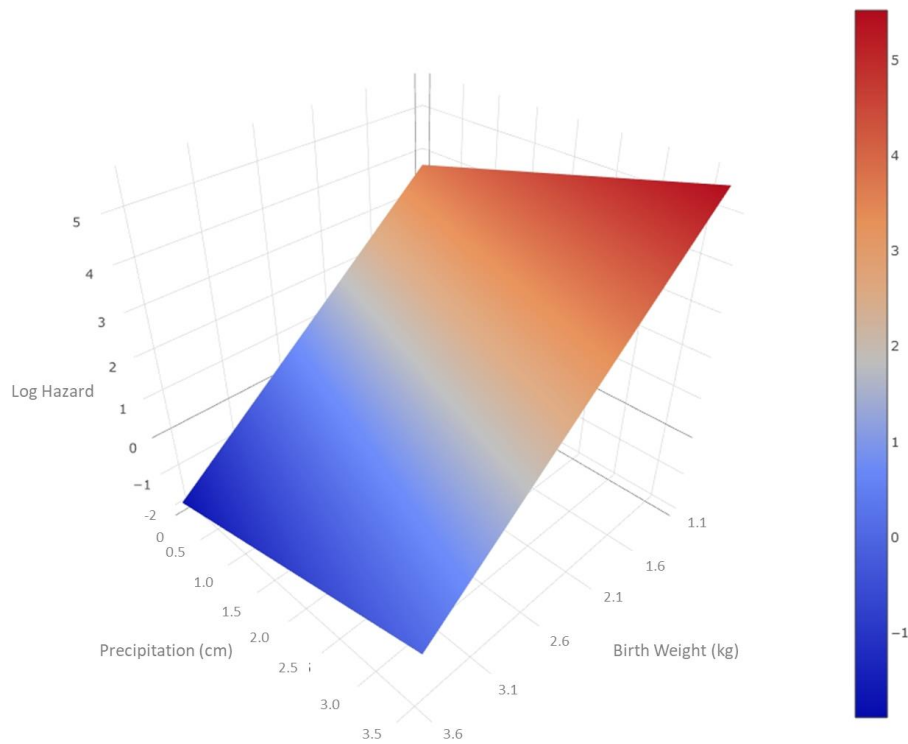


Figure 5 The influence of birth weight and daily precipitation on the risk of mortality in the first 7 days of life for neonates captured in Sussex County, Delaware, USA (2016 and 2017). Log hazard (i.e.; β coefficient) graphed as the response variable to changes in covariate values.

The model of birth weight ($\beta = 0.11$; CI = 0.04 - 0.32) and doe maturity ($\beta = 0.33$; CI = 0.09 - 1.24) predicted that having a mature female as a mother reduced the mortality risk of neonates by 67%. Furthermore, mature females were more successful at raising lower birth weight neonates. Baseline hazard for mature females was a 2.65 kg birth weight, whereas baseline hazard for immature females was 3.15 kg (Figure 6).

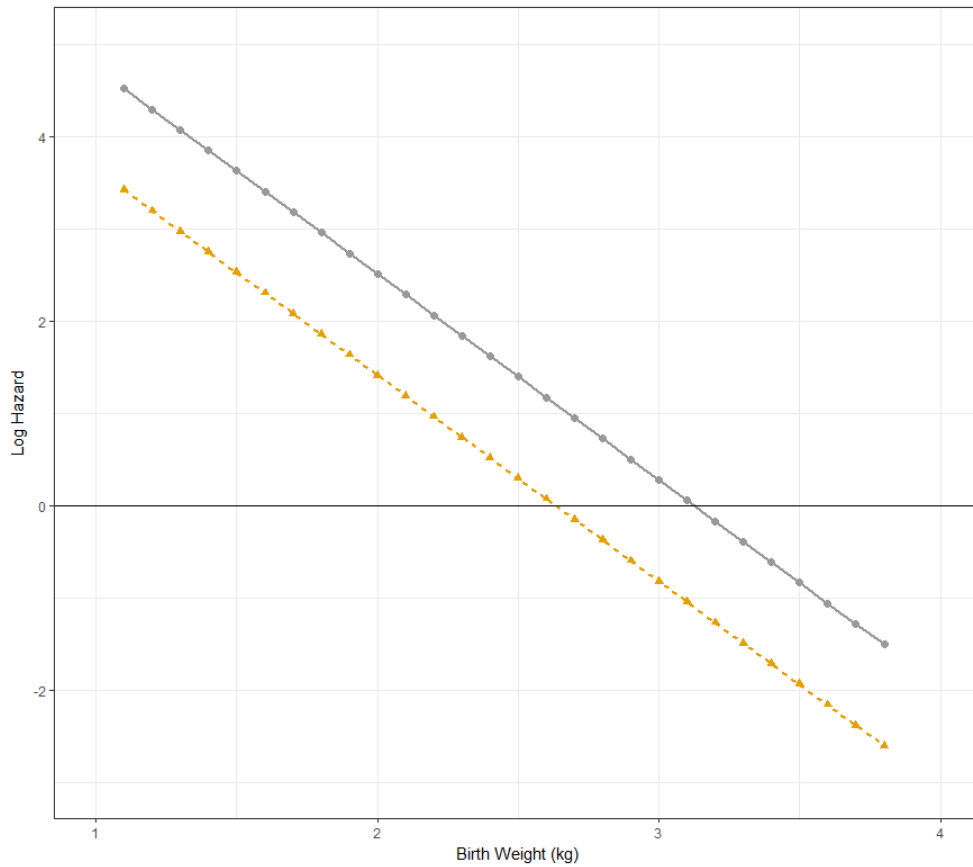


Figure 6 The influence of birth weight and doe maturity on the risk of mortality in the first 7 days of life for neonates captured in Sussex County, Delaware, USA (2016 and 2017). Log hazard (i.e.; β coefficient) graphed as the response variable to changes in covariate values. Mature females represented by the dashed line (orange triangles) and immature females represented by the solid line (grey circles).

For the 30-day window, birth weight and doe maturity were important covariates and birth weight appeared in both competing models (Table 7). Birth weight as a univariate model ($\beta = 0.32$; CI = 0.10 – 1.04) predicted that for every 1 kg increase in a neonate’s birth weight, the instantaneous mortality risk decreased by 68%.

Table 7 Summary of AICc values generated by Cox proportional hazard 30-day survival models for neonates captured in Sussex County, Delaware, USA (2016 and 2017). Depicts the modelled influence of covariates on neonate survival in the first 30 days of life.

Model	AICc	Δ AIC	ω
Birth Weight + Doe Maturity	187.24	0.00	0.43
Birth Weight	188.93	1.69	0.19
Birth Weight + Minimum Temperature	190.11	2.87	0.10
Birth Weight + Precipitation	190.98	3.74	0.07
Birth Weight * Precipitation	191.10	3.86	0.06
Doe Maturity	191.28	4.04	0.06
Birth Weight * Minimum Temperature	192.54	5.30	0.03
Null	192.86	5.62	0.03
Minimum Temperature	194.24	7.00	0.01
Global	194.57	7.33	0.01
Precipitation	194.70	7.46	0.01
Precipitation + Minimum Temperature	196.27	9.03	0.00
Precipitation * Minimum Temperature	198.81	11.57	0.00
Birth Weight* Precipitation * Minimum Temperature	202.74	15.50	0.00

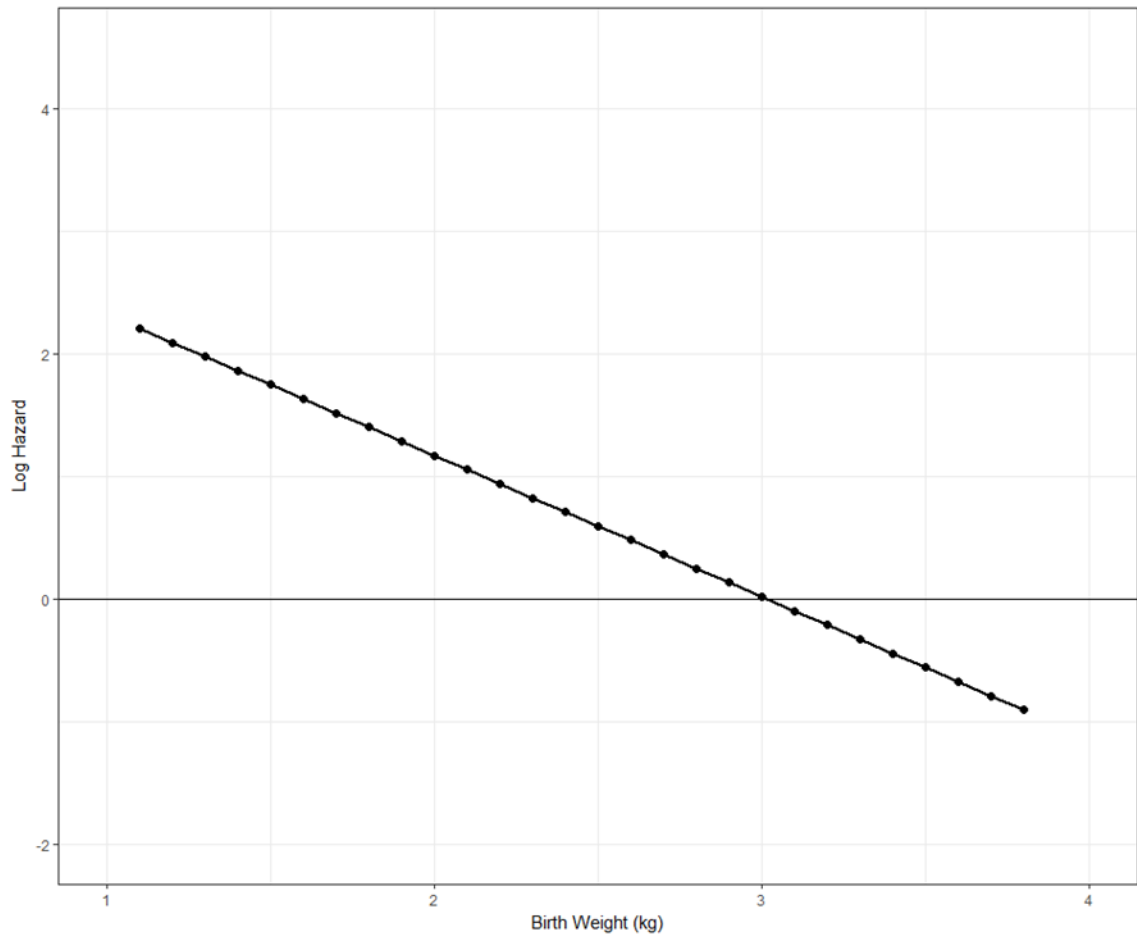


Figure 7 The influence of birth weight and doe maturity on the risk of mortality in the first 30 days of life for neonates captured in Sussex County, Delaware, USA (2016 and 2017). Log hazard (i.e.; β coefficient) graphed as the response variable to changes in covariate values.

The birth weight ($\beta = 0.32$; CI = 0.10 – 1.03) and doe maturity ($\beta = 0.76$; CI = 0.28 – 2.03) model predicted that having a mature female as a mother reduced the instantaneous mortality risk of neonates by 63%. Additionally, mature females were more successful at raising lower birth weight neonates. Baseline hazard for mature

females was at a birth weight of 2.45 kg, while baseline hazard for immature females was at a birth weight of 3.35 kg (Figure 8).

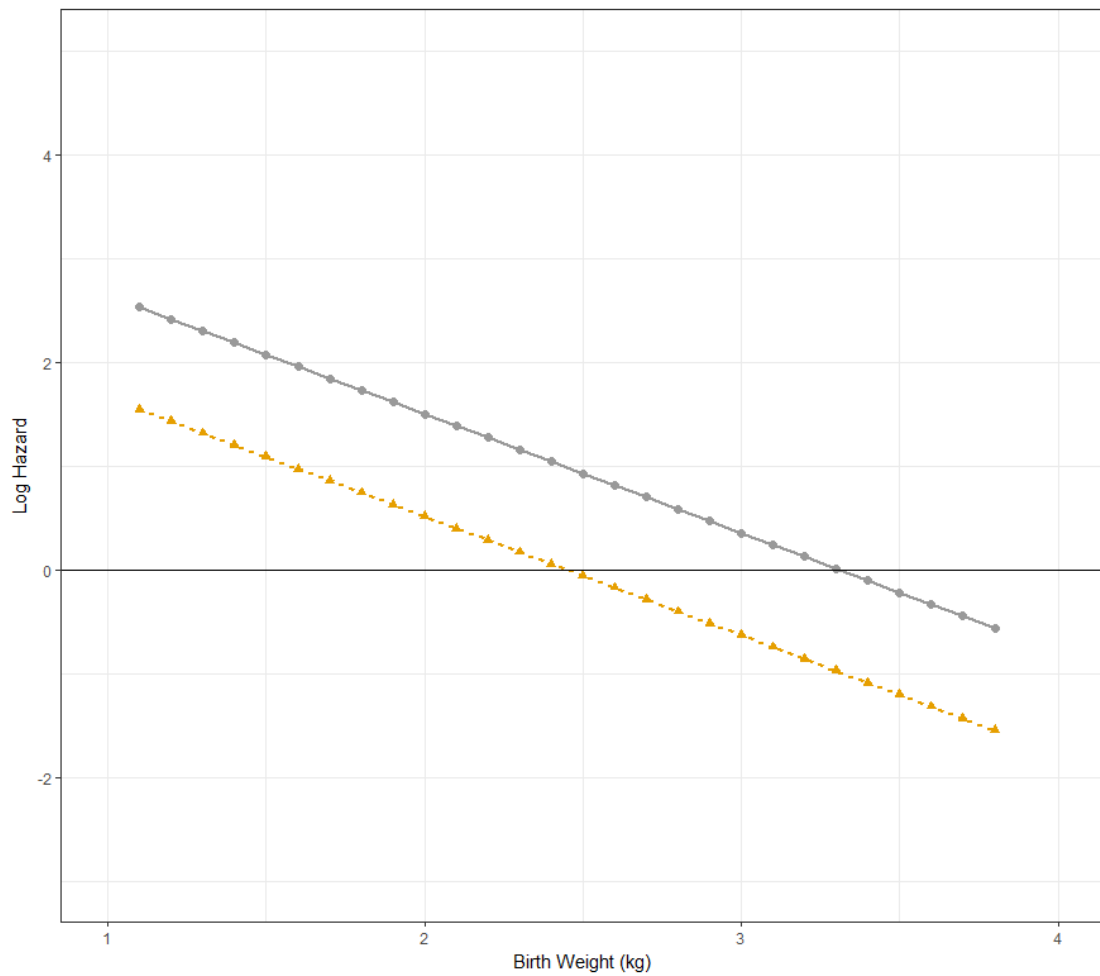


Figure 8 The influence of birth weight and doe maturity on the risk of mortality in the first 30 days of life for neonates captured in Sussex County, Delaware, USA (2016 and 2017). Log hazard (i.e.; β coefficient) graphed as the response variable to changes in covariate values. Mature females represented by the dashed line (orange triangles) and immature females represented by the solid line (grey circles).

Discussion

Throughout nearly all of eastern North America, deer exist in a landscape rich with neonatal predators. To fully understand the effects of predation on neonatal survival, research must be conducted in areas where deer exist in the absence of predators. My estimates of neonatal survival were comparable to survival estimates in other studies from the eastern United States within the past 20 years. My findings demonstrate that without established neonatal predator populations, fawn mortality rates are similar to those where predation is reported as the primary source of mortality.

Natural mortality has been listed as the second greatest source of mortality for neonates in many studies over the past 20 years, with many studies reporting natural mortality rates of 7.8—34.6% of the total mortality observed. Most (83%) of the mortality in my study was natural mortality and the rate is likely greater since I was unable to determine the cause of mortality in 17% of the cases. Emaciation was a major cause of mortality for neonates in Sussex county, but is only reported as a minor contributor to overall mortality in the neonatal survival literature (Carstensen et al. 2005, Saalfeld and Ditchkoff 2007, Chitwood et al. 2015, Shuman et al. 2017). In these studies, emaciation is often linked to abandonment. I do not suspect abandonment was the cause of the observed cases of emaciation. For 62% (n = 13) of the emaciations observed in my study, the necropsies reported milk in the stomach. Additionally, hourly locations of my females suggested that they were still in close proximity to my fawns. I suspect that the emaciation was caused by undetected pathogens. Bacterial sepsis and pneumonia were observed in my study, as well as many past neonatal survival studies (Wickham et al. 1993, Vreeland et al. 2004, Burroughs et al. 2006). These diagnoses require a histological analysis of the neonate,

which are seldom conducted in neonatal survival studies. As a result of submitting my neonates for postmortem histological analysis, PADLS was able to isolate and identify 6 cases of *Theileria cervi* parasitism. Carried by lone-star tick (*Amblyomma americanum*), *Theileria cervi* is commonly found in healthy individuals, but can lead to death in nutritionally stressed individuals or at high levels of infestation (Yabsley et al. 2005, Haus et al. 2018). *Theileria cervi* is difficult to identify, even with histological examination, meaning it could be more prevalent than my findings suggest (Haus et al. 2018). The expansion of lone-star tick ranges could result in greater frequency of infection and mortality of neonates (Springer et al. 2015).

The role of natural mortality as an ultimate source of mortality could be severely understated in the literature. My findings show that natural mortality is prevalent in white-tailed deer populations but is likely being masked by predation as a proximate cause of mortality. Fawns suffering from disease and starvation have been observed exhibiting frequent loud vocalizations indicating they are in distress, which drastically increases the likelihood of discovery by predators (Chitwood et al. 2014). In these cases, the predator is removing animals that would have likely succumb to other natural causes of mortality, which causes predation in these cases to be more compensatory than additive. For managers concerned about declining deer numbers, identification of the ultimate mechanisms causing the declines is critical to the success of management strategies. Predation has dominated the neonatal survival literature as the most important source of mortality in nearly every system containing predators. The over emphasis of predation in such studies has sidetracked management strategies and distracted us from examining other influential variables effecting neonate survival.

Many studies recognized the inclusion of opportunistically captured fawns as a possible source of age bias in neonatal survival studies (Rohm et al. 2006, McCoy et al. 2013, Shuman et al. 2017). Opportunistic capture under-samples the youngest age classes, resulting in a misrepresentation of important mortality sources (Chitwood et al. 2017). Furthermore, left-truncated (i.e.; reduced sample size at the youngest ages) sampling distributions in survival studies can yield inflated survival estimates out to approximately 30 days and cause cascading effects for further survival estimates (Gilbert et al. 2014). My survival estimates demonstrated that opportunistically captured neonates had greater survival rates than those captured using VITs. This difference is explained by high rates of mortality in the first 7 days of life. Similar to other neonatal survival studies, I observed 47% of the mortality in this timeframe (Shuman et al. 2017). With an average age at capture of 6 days old, most opportunistically captured fawns had already survived through the period of greatest mortality. These findings demonstrate that using opportunistically captured fawns will inflated survival estimates.

Survival rates are influenced by both physiological and climatic variables. Birth weight has been well established as an indicator of survival potential for neonates (Mech and Mcroberts 1990, Saalfeld and Ditchkoff 2007, McCoy et al. 2013). My data demonstrated that birth weight was influential on survival but is most influential in the first 7 days of life when neonates are the most vulnerable. Birth weight can also compound the influence of other covariates, such as weather. Heavier neonates may be more resistance to external factors that would weaken smaller, lighter neonates. Birth weight is determined by several maternal characteristics, but one of the most important is maternal age (Adams 2005, Michel et al. 2015).

Maternal characteristics have been reported to influence survival and predation risk for neonates (Ozoga and Verme 1986, Adams 2005, Michel et al. 2015). VIT technology allows researchers to connect each fawn to its maternal female; enabling them to explore how maternal characteristics (e.g.; condition, maturity, etc.) influence neonatal survival. Doe maturity has been linked with neonatal survival under the assumption that mature females are larger and better nutritional condition which leads to larger healthier fawns (Adams 2005, Michel et al. 2015). Furthermore, mature females are seen as more experienced and therefore better able to supplement and protect their offspring (Ozoga and Verme 1986, Mech and McRoberts 1990, Benton et al. 2008, Steiger 2013). Mature females are also more dominant compared to immature females and therefore would occupy the best fawning habitat (Ozoga et al. 1982, Michel et al. 2015). Neonates are dependent on the quality of the habitat, especially in the first weeks of life, to provide bed sites that will offer optimal concealment and shelter (Grovenburg et al. 2010). Neonates born to mature females in my study experienced a lower risk of mortality, and mature females were better able to rear neonates with lower birth weights. The baseline hazard, or the point at which birth weight has no influence on survival, is nearly 1 kg lower for mature females compared to immature females. Changes in birth weight heavily influences overall risk of mortality when combined with other influential covariates, including weather covariates.

Precipitation and minimum temperature were good predictors of neonatal mortality risk in the first 7 days of life for neonates in southern Delaware. Previous research has reported similar relationships, with precipitation presence and minimum temperature negatively influencing neonatal survival at a landscape scale (Ginnett and

Young 2000, Warbington et al. 2017, Michel et al. 2018). Presence of precipitation was reported to increase daily risk of mortality by a factor of 3 at one study site in Wisconsin but had little influence on survival at the second study site (Warbington et al. 2017). Similar geographically dependent effects were found in a Texas study, where precipitation had a negative relationship with survival in east Texas and a positive relationship in the more arid west Texas (Ginnett and Young 2000). During the first 7 days of life, neonates are at their most vulnerable and may be especially susceptible to conditions in their environment such as precipitation and temperature, which impact a fawn's ability to effectively thermoregulate (Grovenburg et al. 2010). Increased thermoregulatory requirements lead to increased expenditures of energy which can draw-down the already limited resources of smaller neonates (Putman et al. 1996, Mysterud and Ostbye 1999). Increased birth weights result in larger energy reserves which could allow neonates to compensate during precipitation event. My findings demonstrate that as the amount of precipitation increases, the required birth weight to neutralize the thermoregulatory effects of that precipitation increases. A similar relationship was seen with minimum temperature and birth weight but it did not appear in any competitive models. Regions that experience more substantial temperature extremes may find that minimum temperature is more influential on neonatal survival than my data suggested.

Management Implications

Use of opportunistic capture methods in assessments of neonatal survival results in inflated estimates and should be avoided in future studies. My findings show that natural mortality is likely the ultimate mechanism influencing neonatal survival rates. Management strategies aimed at increasing neonate survival should be focused

on habitat improvement. Managing habitat for adequate, year-round forage for females so that they are in proper condition as they enter into the gestation and lactation periods. Furthermore, using principles from well establish harvest management strategies such as Quality Deer Management (QDM; Hamilton et al. 1995), I can augment the age structure of females and, perhaps influence neonate survival. My findings, with regards to the influence of doe maturity, show that I can build on the QDM principles in a way that can help direct deer population growth. By protecting older females on the landscape, I ensure that the portion of the population that is most successful at rearing fawns survive into the fawning season. Conversely, by targeting mature females on the landscape, I can compound the ability of annual doe harvests to control population growth by removing the females who are most likely to have success rearing fawns into the population.

Chapter 2

SPATIAL ECOLOGY OF ADULT FEMALE WHITE-TAILED DEER DURING THE FAWNING SEASON

The fawning season is the period of greatest physiological and behavioral change for female white-tailed deer (*Odocoileus virginianus*). Changes in spatial behaviors are primarily driven by pregnancy and fawn rearing (Bertrand et al. 1996, D'Angelo et al. 2004, Gilman et al. 2010, Soto-Werschitz et al. 2018). During late gestation, gravid females experience elevated nutritional and somatic stress as the fetus enters the final stages of development. Increases in stress have been linked to increase in diel home range size in the weeks before parturition, referred to as 'pre-partum restlessness' (D'Angelo et al. 2004). However, a similar study documented a decrease in home range size prior to parturition as females began to actively exclude other females and defend established parturition sites (Ozoga et al. 1982, Bertrand et al. 1996). Gravid females exhibit aggressive behavior toward sympatric females, including non-gravid individuals and previous offspring (Schwede et al. 1993). These behaviors are territorial responses which diminish as the females moves further from their core area (i.e., parturition site and neonate bedding sites; Schwede et al. 1993). Following parturition, isolation behavior persists both as a predator avoidance strategy and to strengthen the bonds between the female and her offspring (Bertrand et al. 1996).

Another method of predator avoidance used by maternal females is the 'hider' strategy. The 'hider' strategy involves females leaving their offspring concealed and unattended for long periods as they forage for food, returning every few hours to nurse (Ciuti et al. 2005, Barbknecht et al. 2011). During the early weeks of the post-parturition period, neonates remain in bedding areas within the mother's home range

with infrequent and small movements from one bed site to another (Ciuti et al. 2005). A study in Minnesota found that neonate moved an average of 66 m between consecutive bed sites, totaling a mean distance 162 m in the first 4 days of life (Carstensen Powell et al. 2005). Eventually fawns will begin to follow their mother throughout her daily activities (Ozoga et al. 1982, Ciuti et al. 2005). The progression of fawns beginning to follow the female is not well documented in the literature. Observational studies using sightings of females with fawns have shown that frequency of interactions increase with the most frequent occurrences after 30 days post-parturition (Ozoga et al. 1982, Hirth 1985).

Observational studies have identified general trends in the behavior of maternal females during the fawning season, but many questions remain unanswered. My objectives were to 1) examine how home range size for maternal females changes throughout the fawning season and 2) investigate changes in doe-to-fawn proximity following parturition.

Study Area

I conducted my research in Sussex County, Delaware (Figure 1). Bordering Sussex County is the Atlantic Ocean (east), Kent County, Delaware (north), and Maryland (south and west). Land use in the county was agriculture (41%), upland forest (22%), forested wetland (22%) and development (15%) (National Agricultural Statistical Service 2012). The major agricultural crops included corn, soybeans, and winter wheat (National Agricultural Statistical Service 2012).

Sussex County has deer densities of about 19 deer/km² and has no established deer predator communities, aside from humans (Delaware Division of Fish and Wildlife 2010). Coyotes are rare in Sussex County; since the state opened a hunting

and trapping season in 2014 only 9 have been harvested according to mandatory reporting data (Rogerson; unpublished data). No confirmed black bear or bobcat sighting have occurred in Sussex County for over 100 years. The only carnivores large enough to prey upon neonates were red fox (*Vulpes vulpes*).

Average annual precipitation during the study was 122 cm; similar to the 30-year (1981–2010) average of 119cm. Temperatures during the study (2015-2017) ranged from -14°C to 36°C (National Climatic Data Center 2012). Spring and Summer precipitation averaged 78 cm, with temperatures ranging from 2°C to 36°C (National Climatic Data Center 2017).

Methods

Adult Capture

I captured adult females from December to April, 2015 – 2017 using rocket nets, drop nets, and clover traps baited with whole kernel corn (Schemnitz et al. 2012). Once captured, I blindfolded and physically restrained individuals, then chemically immobilized using an intramuscular injection of xylazine (0.5mg/kg; Rhoads et al. 2013). I monitored vital rates at 5-minute intervals to ensure the health of each individual during the work up process. I marked each deer with unique numbered ear tags (one plastic and one metal in each ear). I estimated the age of each deer using tooth replacement and wear (Severinghaus 1949). I fit all females ≥ 1.5 years of age with collars and vaginal implant transmitters (VITs) from Advanced Telemetry Systems (Isanti, Minnesota). I deployed Neolink GPS collars (G2110E2 Iridium collars [800gr]) with VITs (M3930U [23gr]) on 44 females and standard VHF collar (M2230B [190gr]) with VITs (M3930 [21.5gr]) on an additional 8 females. I followed

guidelines for VIT deployment established in Bowman and Jacobson (1998) and Carstensen et al. (2003). Following data collection, I administered an intramuscular injection of tolazoline (4mg/kg; Miller et al. 2004) to reverse the effects of the xylazine. I monitored animal condition and vitals, until recovery and individuals left the capture site under their own power. University of Delaware Institutional Animal Care and Use Committee approved all of my capture and handling procedures (#1288).

Location Data Collection

I received GPS location fixes once per day until 1 May. Following 1 May, I received hourly locations via a preprogrammed fix change command. Hourly location fixes continued until 15 June, after which collars recorded a location every 4-hours. Following a birth event, I received an email indicating that the VIT had been expelled. Once located, I weighed and measured each fawn, as well as attached an expandable VHF collar (M4210 [63gr], Advanced Telemetry Systems; Isanti, Minnesota, USA) and uniquely numbered ear tags. Once the work up was complete, I returned fawns to their bedsite and left the area as quickly as possible. I triangulated fawns on an age-based schedule with the most frequent monitoring occurring in the first 30 days of life, starting the day following capture and marking. I located fawns 2 times per day for the first 30 days, once per day from 30 to 60 days, and 3 times a week from 60 to 90 days. I generated location estimates from my triangulation data using a macro program in Microsoft Excel (John Carey, Madison, WI; Radio-Tracker). I accepted location estimates with error estimates of <5,000 m².

Data Analysis

To investigate the impact of caring for fawns on female home range size, I generated 2 average home range data sets; females caring for fawns and females no longer caring for fawns. I generated 7-day home ranges for maternal females using a 95% Kernel Density Estimator (KDE) in program R using the 'adehabitatHR' package. To construct a home range, I required ≥ 20 GPS fixes within the 7-day window. I generated 4 pre-parturition ranges and 13 post-parturition ranges that began on the day of parturition, for a total of 17 home ranges. In the pre-parturition windows, I averaged home range size for each 7-day window across all individuals and graphed the resulting average. Following parturition, I began accounting for loss of fawns by separating home range estimates into 2 different data sets to be averaged. Once all fawns of a female had died, I removed her home range estimates from that week's average home range calculation. I added the females home range estimate for the following week, and every subsequent week, into a separate data set to be averaged and graphed separately from females still caring for fawns. By doing so, I generated 2 average home range lines on my graph; females with living fawns and females after losing fawns (Table 8). Using the average home range estimates for females with living fawns, I looked at the influence of maturity on home range size throughout the fawning season. I used only estimates from females with living fawns so that I could accurately depict differences in maternal care between maturity classes. I characterized females as mature if they were > 4 years old at parturition, and as immature if they were ≤ 4 years old (Lesage et al. 2001, Ditchkoff 2011). I averaged home range estimates by maturity status for each 7-day window and graphed my results.

Table 8 Change in weekly sample size of adult female white-tailed deer captured in Sussex County, Delaware, USA (2016 and 2017). Groupings based on ‘living’ or ‘dead’ designation of neonates.

	Weeks												
	1	2	3	4	5	6	7	8	9	10	11	12	13
No Living Fawns	0	4	5	8	8	9	10	10	10	11	11	12	12
Living Fawns	20	19	16	16	16	15	15	15	14	14	13	13	13
Mature	6	6	6	6	6	6	6	6	5	5	5	5	5
Immature	14	13	10	10	10	9	9	9	9	9	8	8	8

To better understand when fawns begin to follow their mothers and join them in daily excursions, I used location data from both the females and fawns to calculate mother-to-fawn proximity distance. Using package ‘wildlifeDI’ in program R, I generated Euclidian distance estimates between temporally linked locations of the female and her offspring. I considered fawn locations to be linked if the location was taken within 59 minutes of the GPS fix time-stamp of the maternal doe. Using the distances between linked point, I generated mother-to-fawn proximity distance estimates for each day following parturition. I averaged the proximity distance for each day across all fawns and, using Holt-Winters exponential smoothing method, graphed my resulting smoothed proximity distances for the first 90 days of life. To visualize the influence of maturity status on mother-to-fawn proximity distance, I separated females by maturity designation and averaged daily proximity distance for mature and immature females. I graphed the resulting averages to identify any evidence of spatial behavior differences between females of different maturity designations.

Results

Twenty-four GPS collared females gave birth to 42 fawns in the summers of 2016—2017. From 4 weeks pre-partum to 13 weeks post-partum I collected 107,929 locations on maternal females and 6,244 locations on fawns. My estimated weekly home range size ranged from 1.7 to 283.3 ha (Figure 9, Table 8). Average home range size in the 4 weeks prior to parturition was relatively stable, ranging from 51.2 ha to 62.0 ha. Females caring for fawns decreased their average home range size in the first 2 weeks following parturition. The smallest average home range size was observed in the second week following parturition ($\bar{x} = 25.1$ ha). Following week 2, average home ranges began to increase towards pre-parturition sizes. Following week 6, home ranges returned to pre-partum sizes and remained constant until week 13.

For females no longer caring for fawns, I observed a substantial increase in home range in the week following the loss of the fawns (Figure 9). Average home range size spiked at week 3 as a result of increase neonate losses in week 2. Following an initial spike at week 3, average home range decreased and remained at pre-partum sizes until the end of the monitoring period (Figure 9).

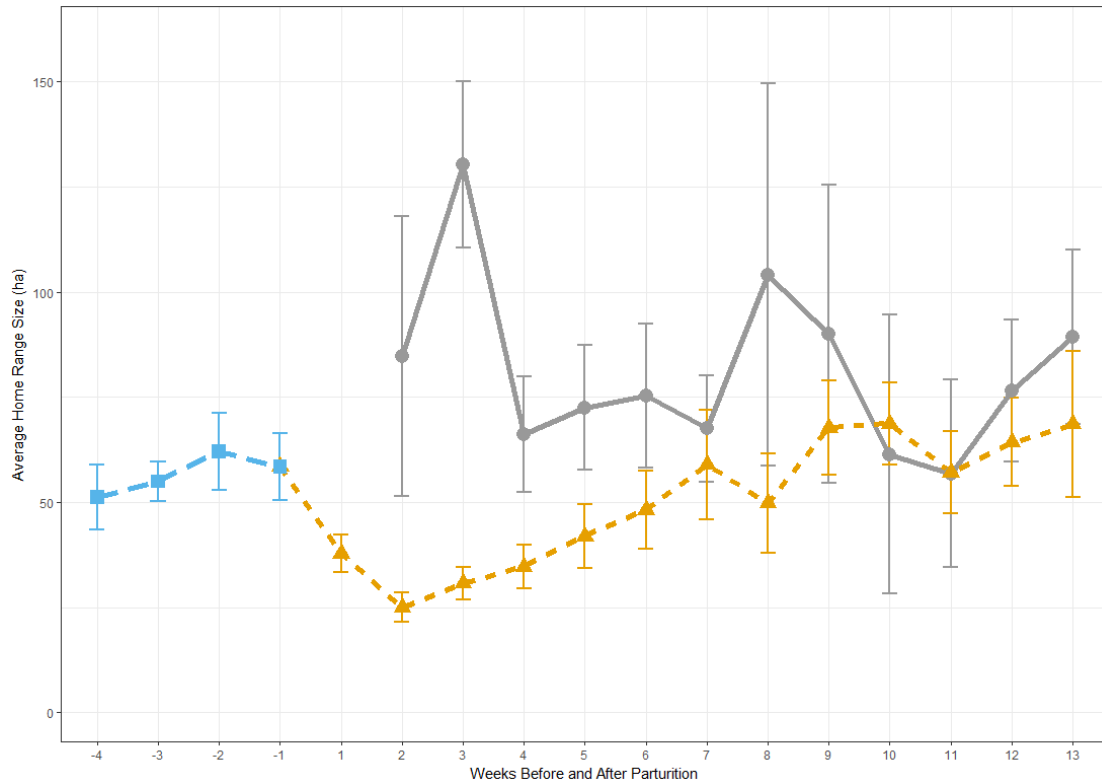


Figure 9 Average weekly (7-day) home ranges size (\pm SE) for pre- (-4 to -1) and post-parturition (1 to 13), with week 1 beginning on the day of parturition. Once a female had lost all fawns, her home range estimate from that week was removed from the “Home Range with Living Fawns” (orange dashed line with triangles) line and added to the “Home Range After Losing Fawns” (grey solid line with circles) line the following week. Pre-parturition period denoted by blue dashed line with squares.

Average mother-to-fawn proximity decrease in the first 4 weeks following parturition (Figure 10). The smallest proximity was observed in week 4 ($\bar{x} = 257.7$ m). Following week 4, mother-to-fawn proximity remained constant until the end of the monitoring period.

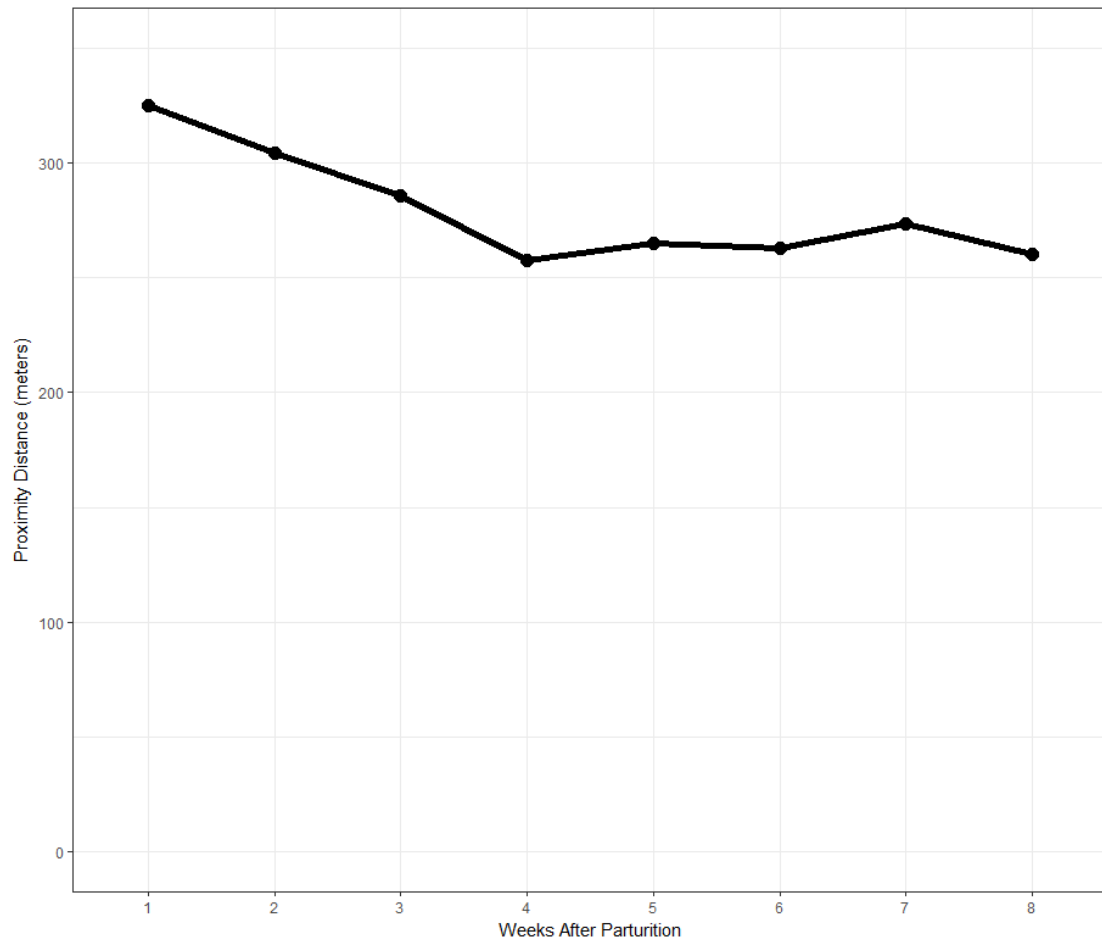


Figure 10 Average weekly doe-to-fawn proximity distance following parturition with Holt-Winters smoothing.

Mature females occupied smaller home ranges in both the pre- and post-parturition periods (Figure 11). Change in home range size was similar for both mature and immature females with the smallest home ranges observed in week 2. Home ranges of mature females remained smaller until week 7, when they exceeded those of immature females. Home range for immature females leveled off following week 6, while mature female home ranges continued to increase until week 10.

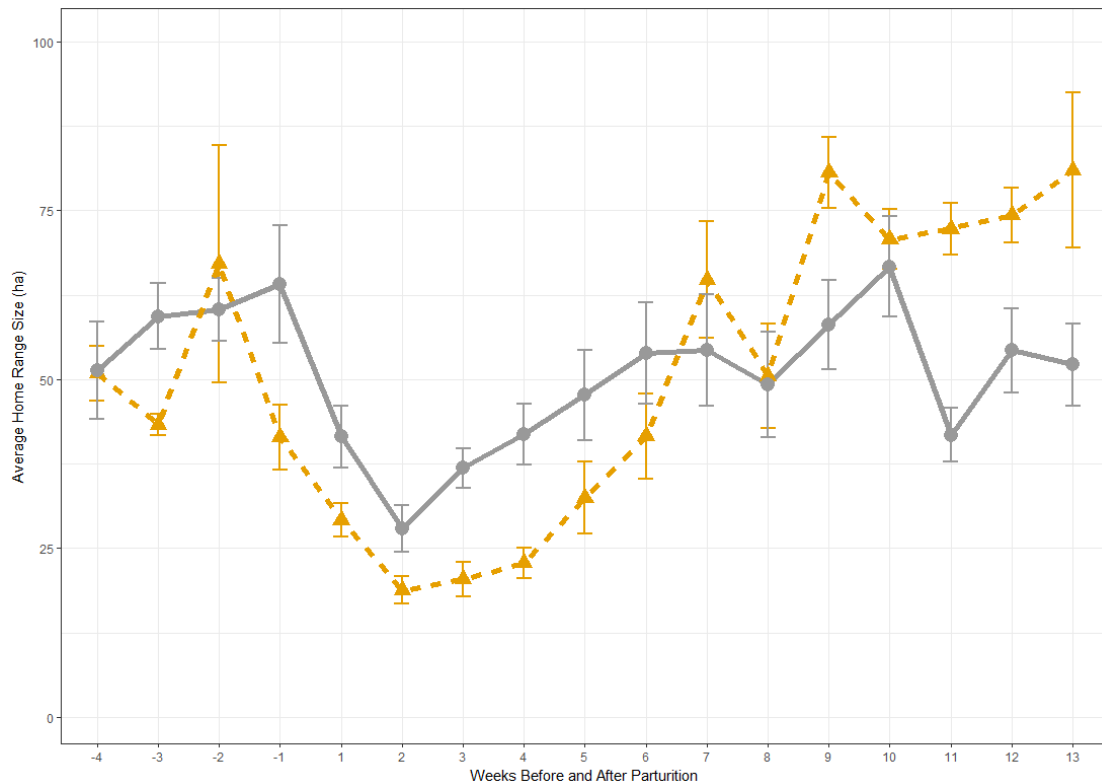


Figure 11 Average weekly (7-day) home ranges size (\pm SE) for pre- (-4 to -1) and post-parturition (1 to 13) by doe maturity status, with week 1 beginning on the day of parturition. Females designated as mature if > 4 years old at parturition. Mature status represented by orange dashed line with triangles and immature status represented by grey solid line with circles.

Mature females remained closer to their neonates in the first 5 weeks following parturition than immature females (Figure 12). Mature female reached their smallest proximity at week 4 (\bar{x} = 221 m). Following week 4, proximity distance began to increase for mature females and continued to increase out to 8 weeks. Immature females remained further from their neonates during the first 5 weeks following parturition (Figure 12). Proximity decreased continuously over the 8-week monitoring

period. Immature female were in closest proximity to their fawns in week 8 ($\bar{x} = 231.7$ m).

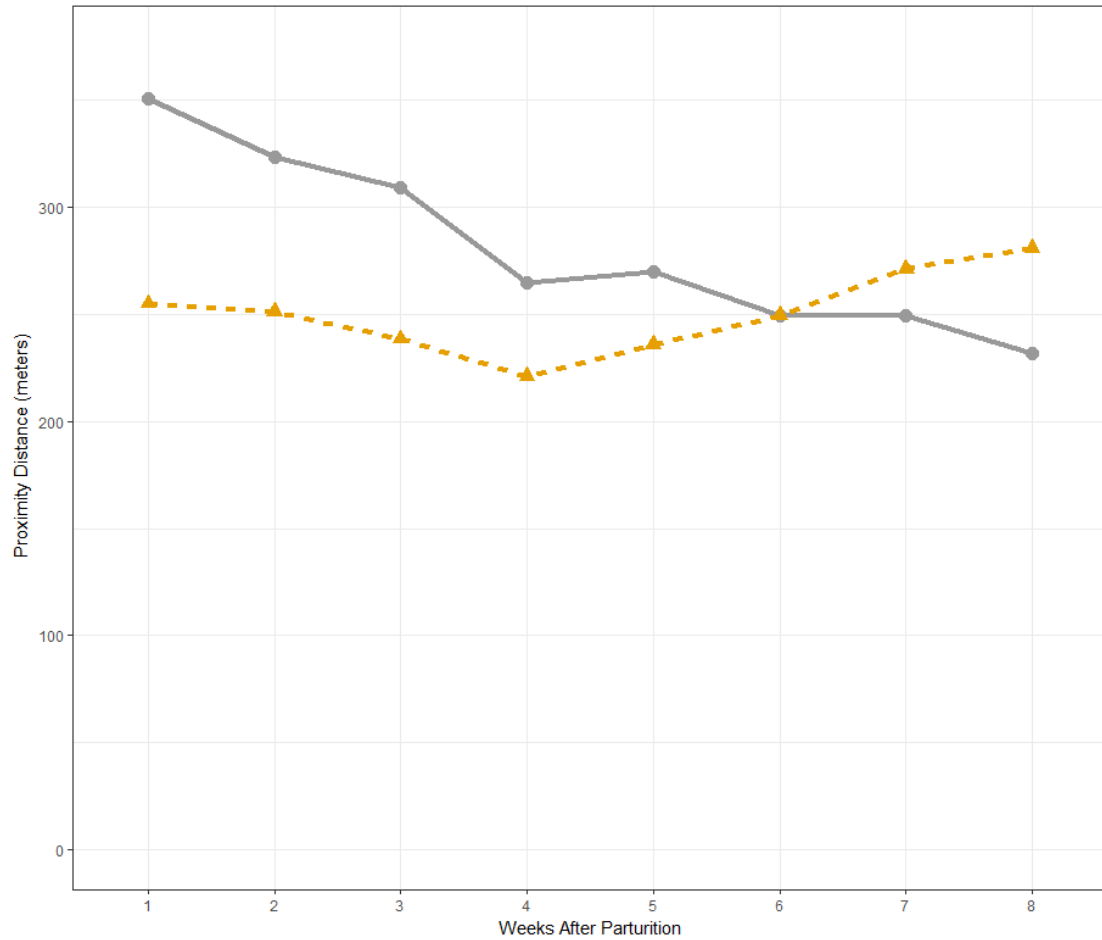


Figure 12 Average weekly mother-to-fawn proximity distance by doe maturity status following parturition with Holt-Winters smoothing. Females designated as mature if greater than 4 years old at parturition. Mature status represented by orange dashed line with triangles and immature status represented by grey solid line with circles.

Discussion

My findings demonstrate home range size for adult females was greatly affected by parturition and the presence of living fawns. Parturition has been shown to influence home range size in both captive (Ozoga et al. 1982) and wild herds (Nixon et al. 1992, Schwede et al. 1993). Female white-tailed deer in agricultural landscapes occupy smaller home ranges following parturition (Nixon et al. 1992). The female deer in my study exhibited similar range restriction observed in post-partum females in previous studies (Ozoga et al. 1982, Nixon et al. 1992, Schwede et al. 1993). Changes in home range size post-partum are often attributed to isolation behavior between parturient females (Ozoga et al. 1982, Schwede et al. 1993, Bertrand et al. 1996). Home range overlap between sympatric females decreases by 90 percent in the first 6 weeks following parturition as a result of isolation behavior (Schwede et al. 1993). Females also isolated themselves from their kin, avoiding interactions for the first 4 to 6 weeks of life (Ozoga et al. 1982). My findings fit with the slow increase of interactions between females eventually returning to normal social interaction after 4 to 6 weeks. Isolation behavior also explains the behavior exhibited by females in my study who lost their fawns.

Females who lost the entire litter of fawns showed an immediate increase in home range size. Studies have reported that unsuccessful mothers almost immediately attempt to socialize with other females following the loss of their fawns (Ozoga et al. 1982). Females who lose their fawns early in the fawning season are often excluded by females who are caring for fawns (Ozoga et al. 1982, Bertrand et al. 1996). The active exclusion by other females until 4 to 6 weeks following parturition is a likely explanation for the uncharacteristically large home ranges for females who lose their fawns early after fawning. The end of antisocial behavior coincides with increases in

interactions between family groups, including fawns of the year (Ozoga et al. 1982, Schwede et al. 1993).

Few studies have examined mother-to-fawn proximity and how proximity changes as the fawn ages and when fawns begin to follow their mothers during her daily activities. Observational studies have provided some insight into when the shift in behaviors may occur based on physical sightings of fawns and females together. The general consensus in these observational studies is that fawns go from spending the majority of their time at bed sites away from their mother, to joining her in her daily activities at 4 weeks of age (Ozoga et al. 1982, Hirth 1985). Proximity estimates for females in my study were larger than observed in previous studies (Ozoga et al. 1982, Carstensen Powell et al. 2005). However, proximity distances have been reported as large as 760 m in the first 2 weeks following parturition (Ozoga et al. 1982) and 460 m in neonates as young as 1-day old (Carstensen Powell et al. 2005). My data showed that proximity (i.e.; distance between the female and an individual fawn) reached its lowest point at 4 weeks post-parturition. The decreased distance likely corresponds with not only increased mobility of the fawns, but the age at which females begin to wean their fawns (Hirth 1985). At about 4 weeks of age, the esophageal groove in the forestomach begins to close (Geist 1998), inhibiting milk consumption and requiring fawns to forage with their mother (Geist 1998). The relationship between the start of the weaning process and changes in spatial behavior has been observed in other cervid species, such as moose (Testa et al. 2000).

Doe maturity strongly influences, not only neonatal survival, but spatial behavior of maternal females during the fawning season (Ozoga and Verme 1986, see Chapter 1). Mature females occupied smaller home ranges in the weeks immediately

surrounding parturition and remained on average closer to their fawns than immature females. Dominant females tend to be the most mature individuals in an area and are the first to select prime fawning habitat (Ozoga and Verme 1986, Michel et al 2015). Dominant females select the highest quality habitat and therefore require smaller home ranges to their resource needs, while less dominant females are actively excluded from these areas (Ozoga and Verme 1986, Bertrand et al. 1996). Immature females must choose lower quality habitats which require greater area to meet the resource needs of the female. The large amount of nutritional resources provided by agricultural landscapes are the likely cause of similar home range size estimates for mature and immature females. Lower quality habitat in an agricultural region still only requires a small amount of space to meet the needs of an individual deer.

Mature females also remained closer to their fawns in the first 6 weeks following parturition. Remaining close to fawns is a well-documented method in which maternal females reduce predation risk (Grovenburg et al. 2012). Studies have demonstrated that neonatal survival was negatively related to average mother-offspring distance due to the decrease ability to defend and frequently nurse the neonate (Tooke 2018). Mature females occupying smaller home ranges and remaining closer to their fawns could explain the greater neonatal survival documented in my study (See Chapter 1).

Chapter 3

BIRTH SITE SELECTION BY FEMALE WHITE-TAILED DEER IN THE FUNCTIONAL ABSENCE OF PREDATORS

Gestation and rearing of offspring are periods of considerable physiological stress for maternal females of many mammalian species including white-tailed deer (*Odocoileus virginianus*; Ciuti et al. 2005, Ditchkoff 2011). Changes during this time are not only somatic and biochemical in nature but behavioral and spatial as well (Bertrand et al. 1996, Bowyer et al. 1999, D'Angelo et al. 2004, Gilman et al. 2010). An immense nutritional and energetic burden is experienced by female deer during the gestation of their offspring, especially during the third trimester when the bulk of fetal development occurs (Schwartz and Hundertmark 1993, Bowyer et al. 1999). During this time, spatial behaviors are likely focused on nutrient intake and sustaining body condition for the duration of the pregnancy.

Immediately prior to parturition, the female must identify a location to give birth to her fawns (Butler et al. 2009). Two primary variables contribute to the selection of a parturition site: forage availability and predator avoidance (Bowyer et al. 1999, Rearden et al. 2011). Sufficient quantity and quality of forage is needed to sustain lactation and female body condition through the rearing period (Bowyer et al. 1999). Without sufficient forage resources the female risks the starvation of her offspring and negatively impacting her own health (Bowyer et al. 1999, Rearden et al. 2011). Predator avoidance pertains both to the female and her offspring. Many studies examining neonatal survival have identified predation as a leading cause of death in white-tailed deer (Ballard et al. 1999, Grovenburg et al. 2011, Kilgo et al. 2012, Jackson and Ditchkoff 2013, Duquette et al. 2014). Good predator avoidance cover is characterized as having high visibility along with adequate escape cover for fawns

(Mao et al. 2005, Rearden et al. 2011). Though maternal females must consider both of these variable when selecting a parturition site, the best areas for predator avoidance are often the areas where forage is of low quality or quantity (Sih 1980, Bowyer et al. 1999, Ciuti et al. 2005). The female must prioritize one variable over the other, resulting in a trade-off (Rachlow and Bowyer 1998, Bowyer et al. 1999, Barten et al. 2001).

To reduce predation risks, cervids employ a ‘hider’ strategy (Ozoga et al. 1982, Ciuti et al. 2005, Barbknecht et al. 2011). ‘Hider’ species conceal their offspring following parturition, leaving them to forage in other areas. The ‘hider’ strategy allows females to travel to areas of higher quality forage without exposing neonates to situation that would increase the risk of mortality (Barbknecht et al. 2011). Females can leave their offspring in areas that provide the greatest amount of cover. Maternal elk (*Cervus elaphus*) selected for less canopy closure at the macrohabitat scale, suggesting selection for greater quantity and quality of forage (Rearden et al. 2011). At the microhabitat scale, maternal females selected for greater canopy closure which resulted in greater visibility (Rearden et al. 2011). Together, these selection decisions made by female elk highlight the multi-faceted nature of parturition site selection.

The loss and subsequent reintroduction of several predator species across the country has prompted examinations of the effects that predation has on behavior of prey species (Blumstein 2002, Mao et al. 2005, Bonnot et al. 2016). Studies have found that following a partial loss of the predator suite (one or more spp.) from a system, predator avoidance behaviors may still exist (Mao et al. 2005, Lahti et al. 2009, Bonnot et al. 2016); a phenomenon known as “the ghost of predators past” hypothesis (Kjellander et al. 2012). Another possible cause of continued predator

avoidance behavior is pleiotropy, which is an anti-predator behavior that persists because it serves an alternative purpose (Kjellander et al. 2012). For example, good predator avoidance cover is often in more closed canopies which also provides thermoregulatory benefits for neonates (Kjellander et al. 2012).

The ‘ghost of predators past hypothesis’, along with the concept of pleiotropy have only been applied to systems where some neonatal predators still exist. As coyotes expand into the few remaining neonatal predator free regions, there are few opportunities to investigate the influence of the absence of predators on prey species (Gompper 2002). My objective was to investigate parturition site selection by adult female white-tailed deer in the functional absence of predators.

Study Area

I conducted my research in Sussex County, Delaware (Figure 1). Bordering Sussex County is the Atlantic Ocean (east), Kent County, Delaware (north), and Maryland (south and west). Land use in the county was agriculture (41%), upland forest (22%), forested wetland (22%) and development (15%) (National Agricultural Statistical Service 2012). The major agricultural crops included corn, soybeans, and winter wheat (National Agricultural Statistical Service 2012).

Sussex County has deer densities of about 19 deer/km² and has no established deer predator communities, aside from humans (Delaware Division of Fish and Wildlife 2010). Coyotes are rare in Sussex County; since the state opened a hunting and trapping season in 2014 only 9 have been harvested according to mandatory reporting data (Rogerson; unpublished data). No confirmed black bear or bobcat sighting have occurred in Sussex County for over 100 years. The only carnivores large enough to prey upon neonates were red fox (*Vulpes vulpes*).

Average annual precipitation during the study was 122 cm; similar to the 30-year (1981–2010) average of 119cm. Temperatures during the study (2015-2017) ranged from -14°C to 36°C (National Climatic Data Center 2012). Spring and Summer precipitation averaged 78 cm, with temperatures ranging from 2°C to 36°C (National Climatic Data Center 2017).

Methods

Adult Capture

I captured adult females from December to April, 2015 – 2017 using rocket nets, drop nets, and clover traps baited with whole kernel corn (Schemnitz et al. 2012). Once captured, I blindfolded and physically restrained individuals, then chemically immobilized using an intramuscular injection of xylazine (0.5mg/kg; Rhoads et al. 2013). I monitored vital rates at 5-minute intervals to ensure the health of each individual during the work up process. I marked each deer with unique numbered ear tags (one plastic and one metal in each ear). I estimated the age of each deer using tooth replacement and wear (Severinghaus 1949). I fit all females ≥ 1.5 years of age with collars and vaginal implant transmitters (VITs) from Advanced Telemetry Systems (Isanti, Minnesota). I deployed Neolink GPS collars (G2110E2 Iridium collars [800gr]) with VITs (M3930U [23gr]) on 44 females and standard VHF collar (M2230B [190gr]) with VITs (M3930 [21.5gr]) on an additional 8 females. I followed guidelines for VIT deployment established in Bowman and Jacobson (1998) and Carstensen et al. (2003). Following data collection, I administered an intramuscular injection of tolazoline (4mg/kg; Miller et al. 2004) to reverse the effects of the xylazine. I monitored animal condition and vitals, until recovery and individuals left

the capture site under their own power. University of Delaware Institutional Animal Care and Use Committee approved all of my capture and handling procedures (#1288).

VIT Monitoring

I located collared females and monitored VIT status weekly following deployment until 6 May. Starting 6 May, I increased the frequency of my location and VIT status monitoring to every 6 hours to ensure timely notification of parturition events (Saalfeld and Ditchkoff 2007, Kilgo et al. 2012, Jackson and Ditchkoff 2013). I remotely received GPS locations and VIT status reports from the GPS collared females once per day until 1 May. Following 1 May, I received GPS locations and VIT status reports every hour. Once I received the notification of VIT expulsion, I dispatched field crews to the site and began to search for the fawns (1 – 2 hours after notification).

Vegetation Sampling and Analysis

Upon locating a birth site, I collared and marked all neonates present. I recorded the location of the birth site and returned to the location within 24 -72 hours to collect vegetation measurements (Butler et al. 2009). For my sampling, I measured horizontal vegetation density, canopy cover, basal area and ground cover. I measured horizontal vegetation density using a Nudds board (Nudds 1977) placed 15 m from plot center in each of the cardinal directions and assessed the horizontal cover (1 meter from ground) because I was measuring density of cover useful to a bedded female and fawns. I estimated canopy cover for the plot using a spherical densitometer at plot center and 15 m away in the 4 cardinal directions. I estimated basal area using 5- and

10-factor prisms. I assessed ground cover by placing a Daubenmire frame (0.5×0.5 m) 5 m from plot center in the 4 cardinal directions and estimating the percent of the 6 cover types (i.e.; bare ground, grass, herbaceous, tree, vines, woody debris).

After completing vegetation sampling at the birth site, I selected an azimuth from lists of randomly generated azimuths ($0^\circ - 360^\circ$). I travelled 200 meters on the designated azimuth and repeated my vegetation sampling (Barbknecht et al. 2011). I used a distance of 200 meters because it was the distance a female could move in 2 – 3 hours during the fawning season, and therefore available to her at the time of parturition (Rhoads et al. 2010). I avoided placing random plots in different habitats from the paired used sited (i.e.; a used site in the forest did not have a paired random site in a row crop field). If this condition was not met by the first azimuth, I selected another and repeated the process. I used a paired t-test to assess differences in vegetation characteristics between used (observed birth sites) and unused sites (random sites). I considered mean vegetation measurements to be statistically different at an alpha level of 0.1.

Results

I sampled 32 white-tailed deer birth sites along with 32 paired random sites. I located 84% ($n = 27$) of the birth sites in mixed upland forest. The remaining sites were located in wet meadows ($n = 2$), hay field ($n = 1$), forested wetland ($n = 1$), and clear cut ($n = 1$).

Basal area (5 and 10 factor), canopy cover, tree cover, vine cover, and woody debris did not differ between observed birth sites and random sites. I observed 8% more horizontal cover at observed birth sites than at random sites. Birth sites had 4%

less bare ground than random sites. Random site had 4% more grass cover than birth sites (Table 9).

Table 9 Summary of results from paired t-test analysis between observed parturition sites and paired random sites. Observed parturition sites identified using locations of VITs implanted in adult females (≥ 1.5 years old) from Sussex County, Delaware, USA (2015 - 2017).

Variable	Observed		Random		Paired t-Test Results			
	\bar{X}	SE	\bar{X}	SE	df	t	p value	Effect Size
Horizontal Cover	59	4.23	51	3.77	30	1.98	0.06	8
Bare Ground	1	0.32	5	2.21	30	-1.86	0.07	4
Grass Cover	8	3.50	12	4.56	30	-1.75	0.09	4
Herbaceous Cover	13	3.46	8	2.06	30	1.57	0.13	5
Woody Cover	11	2.42	7	1.86	30	1.38	0.18	4
Canopy Closure	80	4.62	78	5.35	30	0.71	0.49	2
Basal Area (5 factor)	86	9.77	90	11.29	30	-0.58	0.57	4
Tree Cover	4	1.02	5	1.63	30	-0.54	0.59	1
Basal Area (10 factor)	104	12.63	106	13.48	30	-0.20	0.84	2
Woody Debris Cover	12	2.69	12	2.71	30	0.04	0.96	0

Discussion

Parturient females exhibited selection for vegetation characteristics associated with predator avoidance cover. Females in Sussex county selected for 8% greater horizontal cover at parturition sites when compared to paired random sites. Selection for greater horizontal cover has been reported in parturition studies on other white-tailed deer population, as well as other cervid species (Shuman et al. 2018). Similar selection was documented for Alaskan moose (*Alces alces*); however, the relationship was not statistically significant (Bowyer et al. 1999). Horizontal cover at the

parturition site provides visual obstruction and concealment to females giving birth to fawns and during subsequent nursing (Shuman et al. 2018). White-tailed deer are evolutionarily adapted to areas with greater horizontal cover and obstruction (Geist 1998). Utilizing semi-saltatorial locomotion, white-tailed deer use obstructions to their advantage when escaping predator by bounding over structures which predators cannot navigate (Geist 1998). In addition, horizontal cover can impede the flow of air at the parturition site, resulting in diminished scent dispersal (Shuman et al. 2018). Diminishing scent dispersal limits the ability of predators to detect the olfactory cues from the parturition site, thus decreasing the likelihood of being discovered (Wells and Lehner 1978, Shuman et al. 2018).

Canopy closure is another vegetation characteristic associated with selection of parturition sites. Females select parturition sites with greater canopy closure compared to other sites in her home range (Rearden et al. 2011). Selection for canopy closure for females in my study was not statistically significant and was just 2% greater at parturition sites. Average canopy closure was low for moose at both observed and random sites, suggesting that moose selected areas with greater forage availability (Bowyer et al. 1999). Forest composition likely influenced canopy closure results, with the forested landscape being dominated by planted pine stands of short leaf and loblolly pine (Lister and Widmann 2016). Planted pine stands tend to be relatively uniform in structure and lack variation in vegetation characteristics such as canopy closure (Lister and Widmann 2016).

Genetic behavioral traits such as predator avoidance behaviors can persist longer in the absence of the selective pressure than morphological or physiological traits (Lahti et al. 2009, Bonnot et al. 2016). Behavioral traits have been shown to

change as a result of the loss of a keystone predator on the landscape, but do not disappear altogether. Elk in Yellowstone National Park shifted their selection to less open and recently burned areas with more structure following the reintroduction of wolves (*Canis lupus*) after a 70-year absence (Mao et al. 2005). Predator avoidance behaviors by the elk relaxed in the absence of wolves, but were not lost entirely, enabling them to quickly adjust to the reintroduction of wolves (Mao et al. 2005). Predators of white-tailed deer, other than coyote, have been absent from southern Delaware for as long as state records have been kept. Parturient females in southern Delaware have retained their selection towards some types of predator avoidance cover. My findings show that predator avoidance behaviors are deeply engrained in deer ecology and are still expressed in the absence of predators.

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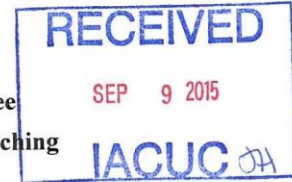
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Appendix

APPROVAL FOR USE OF ANIMALS IN RESEARCH AND TEACHING



University of Delaware
 Institutional Animal Care and Use Committee
 Application to Use Animals in Research and Teaching



Title of Protocol: Fawn Survival of White-tailed Deer in Sussex County, Delaware	
AUP Number: 1288-2015-0	← (4 digits only — if new, leave blank)
Principal Investigator: Dr. Jacob Bowman	
Common Name: white-tailed deer	
Genus Species: <i>Odocoileus virginianus</i>	
Pain Category: <i>(please mark one)</i>	
USDA PAIN CATEGORY: <i>(Note change of categories from previous form)</i>	
Category	Description
<input type="checkbox"/> B	Breeding or holding where NO research is conducted
<input checked="" type="checkbox"/> C	Procedure involving momentary or no pain or distress
<input type="checkbox"/> D	Procedure where pain or distress is alleviated by appropriate means (analgesics, tranquilizers, euthanasia etc.)
<input type="checkbox"/> E	Procedure where pain or distress cannot be alleviated, as this would adversely affect the procedures, results or interpretation

Official Use Only	
IACUC Approval Signature: _____	
Date of Approval: _____	10/2/15

Principal Investigator Assurance

1. I agree to abide by all applicable federal, state, and local laws and regulations, and UD policies and procedures.
2. I understand that deviations from an approved protocol or violations of applicable policies, guidelines, or laws could result in immediate suspension of the protocol and may be reportable to the Office of Laboratory Animal Welfare (OLAW).
3. I understand that the Attending Veterinarian or his/her designee must be consulted in the planning of any research or procedural changes that may cause more than momentary or slight pain or distress to the animals.
4. I declare that all experiments involving live animals will be performed under my supervision or that of another qualified scientist. All listed personnel will be trained and certified in the proper humane methods of animal care and use prior to conducting experimentation.
5. I understand that emergency veterinary care will be administered to animals showing evidence of discomfort, ailment, or illness.
6. I declare that the information provided in this application is accurate to the best of my knowledge. If this project is funded by an extramural source, I certify that this application accurately reflects all currently planned procedures involving animals described in the proposal to the funding agency.
7. I assure that any modifications to the protocol will be submitted to by the UD-IACUC and I understand that they must be approved by the IACUC prior to initiation of such changes.
8. I understand that the approval of this project is for a maximum of one year from the date of UD-IACUC approval and that I must re-apply to continue the project beyond that period.
9. I understand that any unanticipated adverse events, morbidity, or mortality must be reported to the UD-IACUC immediately.
10. I assure that the experimental design has been developed with consideration of the three Rs: reduction, refinement, and replacement, to reduce animal pain and/or distress and the number of animals used in the laboratory.
11. I assure that the proposed research does not unnecessarily duplicate previous experiments. <i>(Teaching Protocols Exempt)</i>
12. I understand that by signing, I agree to these assurances.
<div style="display: flex; justify-content: space-between;"><div style="text-align: center;"> Signature of Principal Investigator</div><div style="text-align: center;"> Date</div></div>