


RESEARCH ARTICLE

Functional Ecology



Relative reproductive phenology and synchrony affect neonate survival in a nonprecocial ungulate

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Abstract

1. Degree of reproductive synchronization in prey is hypothesized as a predator defense strategy reducing prey risk via predator satiation or predator avoidance. Species with precocial young, especially those exposed to specialist predators, should be highly synchronous to satiate predators (predator satiation hypothesis), while prey with nonprecocial (i.e. altricial) young, especially those exposed to generalist predators, should become relatively asynchronous to avoid predator detection (predator avoidance hypothesis). The white-tailed deer *Odocoileus virginianus* in North America is an example of a nonprecocial ungulate that uses the hider strategy early in life; its primary predator (coyote; *Canis latrans*) is a generalist, making white-tailed deer a good model species to test the predator avoidance hypothesis.
2. We used birth dates and known fates of white-tailed deer neonates ($n = 1,032$) across nine study sites varying in relative synchrony and predator assemblages to test the predator avoidance hypothesis. We predicted that relative birthing asynchrony of the population would increase relative survival at the population level; therefore, at the individual scale, neonate birth date nearer to mean birthing date in a respective population would not influence individual survival.
3. Coyotes were responsible for the majority of predation events, and survival of those neonates increased the closer the individual was born to peak birthing season in each respective population. Also, at the population level, reproductive asynchronization negatively affected survival.

4. Contrary to the predator avoidance hypothesis, our data indicate patterns in neonate survival for white-tailed deer better support the predator satiation hypothesis at the individual and population level. Additionally, coyotes may present a selective force great enough to shift reproductive synchrony such that predator satiation may become a feasible defense strategy for neonates at local spatial scales.
5. Our results indicate that synchronizing reproduction may still be the most effective strategy to reduce individual predation risk from generalist predators, particularly when the window of heightened resource availability to the prey is narrow.

KEYWORDS

Odocoileus virginianus, predator avoidance hypothesis, predator satiation hypothesis, reproductive phenology, reproductive synchrony, white-tailed deer

1 | INTRODUCTION

Selective pressures such as nutritional availability and climate affect the evolutionary trajectory of reproductive phenology and synchrony. For example, primary productivity affected conception probability for savanna elephants *Loxodonta africana* (Wittemyer et al., 2007), and in reindeer *Rangifer tarandus*, the early onset of spring combined with increased primary productivity positively affected reproductive success (Tveraa et al., 2013). Moreover, birth phenology shifts when the environment changes as demonstrated in red deer *Cervus elaphus* (Bonnet et al., 2019; Coulson et al., 2003) and reindeer (Paoli et al., 2018) that shifted reproductive phenology in response to climate warming. Although climate seems to primarily govern the timing of reproduction, predation also likely influences synchrony among species within specific populations. For example, in roe deer *Capreolus capreolus*, earliest and latest born neonates (i.e. predator swamping; Darling, 1938) experienced greater mortality from predators, which should stabilize selection for reproductive synchrony within populations (Jarnemo et al., 2004).

Darling (1938) first proposed the predator swamping hypothesis to explain reproductive synchrony (degree of coordination or spread; Sinclair et al., 2000) as a predator defense strategy. Predator swamping, also referred to as predator satiation (Janzen, 1976; Lloyd & Dybas, 1966), is a strategy whereby a prey species synchronizes birthing events to overwhelm predator handling time, reducing per capita neonate predation risk. Some prey species synchronize birth events consistent with the predator satiation hypothesis (mountain goat kids *Oreamnos americanus*, Côté & Festa-Bianchet, 2001; roe deer neonates, Jarnemo et al., 2004) but benefits of that strategy may depend on predator hunting mode. Ims (1990a, 1990b) hypothesized that reproductive synchrony may be the best defense for newborns when facing a specialist predator, whereas asynchrony may be a better strategy for newborns when facing generalist predators. Sinclair et al. (2000) further hypothesized that precocial neonates occurring at high densities and displaying a 'follower' strategy should exhibit increased reproductive synchrony (predator satiation hypothesis), whereas nonprecocial (i.e. altricial) neonates occurring

at low population densities and displaying a 'hider' strategy should exhibit asynchronous births to avoid predation (predator avoidance hypothesis) given they do not occur at densities great enough to satiate predators (Ims, 1990a). Predator avoidance should also be beneficial as it reduces the likelihood that a predator will switch focus to a specific prey species during the parturition season. Although the predator satiation hypothesis has been tested repeatedly, little attention has been paid to the predator avoidance hypothesis even though it is predicted to be the most effective strategy for nonprecocial prey with a generalist predator.

White-tailed deer *Odocoileus virginianus* are widely distributed across differing environments and predator assemblages of North America (Heffelfinger, 2011) and display substantive variation in reproductive synchrony and phenology. For example, populations at northern latitudes can display relatively high reproductive synchrony with 71% of births occurring within 14 days (Michel et al., 2017) in comparison to more southern latitudes where the entirety of a breeding season may differ by as much as 35 days for adjacent populations, presumably allowing for increased asynchrony among adjacent populations (Sumners et al., 2015). Also, white-tailed deer are relatively nonprecocial compared to other ungulates as they use a hider strategy within the first 30 days of life (Carl & Robbins, 1988; Lent, 1974). Coyotes *Canis latrans*, which are generalist predators (Boutin & Cluff, 1989; Gese et al., 1988), are perhaps the primary predators of neonates across their range. Thus, because white-tailed deer are relatively nonprecocial, are exposed to a generalist predator, and display variation in reproductive synchrony, they may be a suitable model species to test the predator avoidance hypothesis.

We compiled birth timing and known fate data for neonate white-tailed deer from nine study areas to test the predator avoidance hypothesis using previously published data from Alabama (31°N; Jackson & Ditchkoff, 2013), Louisiana (32°N; Shuman et al., 2017), Michigan (45°N, Duquette et al., 2014; 46°N, Norton et al., 2018), North Carolina (35°N; Chitwood, et al., 2015), South Carolina (33°N, McCoy et al., 2013; 33°N, Kilgo et al., 2014) and Pennsylvania (41°N; Vreeland et al., 2004), USA. Across these study areas, white-tailed deer experience a relatively wide variation in climatic conditions with

severe winter weather in northern study areas leading to unpredictable timing of spring green up compared to the subtropical climates in southern study areas with more predictable timing of spring green up (Bunnell, 1982; Hardin et al., 1984; Huot et al., 1984). These study areas are populated by a varying suites of predators with varying degrees of dietary specialization. The most common predator was coyote, which along with bobcats *Lynx rufus*, occurred on all nine sites; however, black bears *Ursus americanus* and wolves *C. lupus* also occurred on some sites. Coyotes and black bears are considered primary predators of white-tailed deer neonates where they occur, and both are considered generalist predators (Ballard, 2011; Kautz et al., 2019); thus, they should display a functional response (either a type I or type II functional response depending on the reproductive synchrony of the white-tailed deer population) during the birthing season (Holling, 1959; Krebs, 1978).

Although environmental factors likely govern reproductive synchrony among populations, predator assemblage may also affect reproductive phenology and synchrony within a population. Therefore, we tested the predator avoidance hypothesis using four analytical scenarios: (1) combined all data including unknown predation events and did not differentiate predator species, (2) restricted data to primary predators of neonate white-tailed deer (coyote and black bear predations), (3) restricted data to only coyote predations and (4) restricted data to only black bear predations. Although we restricted analyses to select predator species, neonates at some study areas were exposed to additional predator species in analytical scenarios 2, 3 and 4. We also included latitude to account for the effects of the local

environment on reproductive synchrony. We predicted that population level survival probability would increase with asynchrony of the population (predator avoidance hypothesis; Sinclair et al., 2000) and therefore, survival probability of an individual neonate would not be affected by its birth date relative to the mean of the respective population (predator satiation hypothesis; Darling, 1938; Figure 1).

2 | MATERIALS AND METHODS

2.1 | Study areas

We collected data from nine study sites ranging from 31°N to 46°N and 77°W to 91°W across eastern North America (Figure 2). Study sites displayed a wide range in land cover, land use and environmental conditions.

2.1.1 | Alabama

In Alabama, we conducted research on a 31.6-km² section of Fort Rucker (31.3437°N, 85.7080°W) from 2004 to 2005. Fort Rucker was a 183-km² military facility that conducts helicopter training for the U.S.

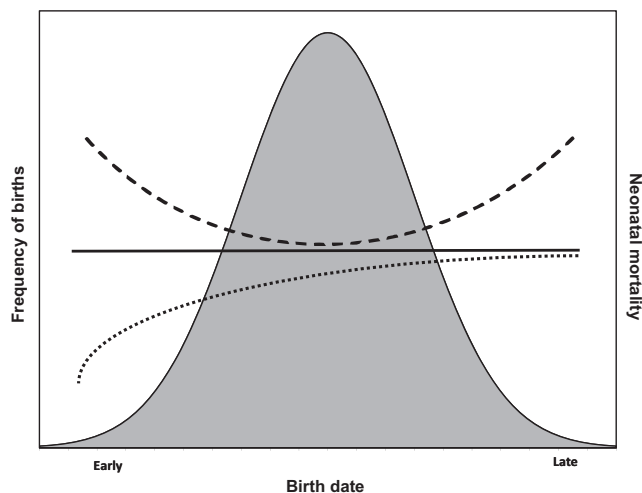


FIGURE 1 Hypothesized relationships depicting how predation may affect neonate mortality rate relative to birth synchrony and birth date, assuming a normal distribution of births (shaded area, primary Y axis). Lines represent neonate mortality rate throughout the parturition season. Dotted line indicates predator swamping is ineffective, because predators improve their search efficiency and increase neonate mortality rate throughout the birthing season. Solid line indicates predation does not affect neonate mortality rate and environmental conditions influence birth synchrony. Dashed line indicates predator swamping is an effective predator defense strategy with neonate mortality rate being least at peak birth timing (secondary Y axis)



FIGURE 2 Study sites where we captured and monitored survival for 1,032 neonate white-tailed deer *Odocoileus virginianus* across eastern North America from 2000 to 2014. (A) Tensas River National Wildlife Refuge, Louisiana (2013–2014); (B) Fort Rucker, Alabama (2004–2005); (C) The United States Department of Energy's Savannah River Site, South Carolina (2007–2012); (D) Brosnan Forest, South Carolina (2006–2010); (E) Fort Bragg Military Installation, North Carolina (2011–2012); (F) Penns Valley, Pennsylvania (2000–2001); (G) Quehanna Wild Area, Pennsylvania (2000–2001); (H) Escanaba, Michigan (2009–2011); (I) Cyrstal Falls, Michigan (2013–2014)

Army. Vegetation was comprised of pine (*Pinus* spp.) and mixed pine-hardwood forests. Deer density was 11.0 deer/km² and potential neonate predators included bobcats and coyotes (Jackson & Ditchkoff, 2013).

2.1.2 | Louisiana

In Louisiana, we conducted research on the Tensas River National Wildlife Refuge and surrounding private lands (hereafter Tensas; 32.3176°N, 91.3771°W) from 2013 to 2014. Tensas was a 57-km² bottomland hardwood site located in northeastern Louisiana in the upper Tensas River Basin. Deer density was 14.0 deer/km² (J. Bordelon, Louisiana Wildlife and Fisheries Department, pers. comm.). Potential predators included coyotes, black bears and bobcats.

2.1.3 | Michigan

We conducted research on two study sites in Michigan. We collected data at the Escanaba study site (45.7452°N, 87.0646°W) from 2009 to 2011. The Escanaba study site was 850-km² in Delta and Menominee counties in the south-central region of the Upper Peninsula of Michigan. Vegetation was comprised of lowland and upland forests. Deer density ranged from 6.4 to 8.4 deer/km² (T. Kautz, pers. comm.). Potential neonate predators included coyotes, black bears, bobcats and wolves (Duquette et al., 2014; Norton et al., 2018).

We also collected data at the Crystal Falls study site (46.0980°N, 88.3340°W) from 2013 to 2014. The Crystal Falls study site was about 1,830 km² in Baraga, Dickinson, Iron and Marquette counties in the Upper Peninsula of Michigan. Vegetation was comprised of lowland conifer forests, deciduous forests and mixed forests. Deer density ranged from 3.0 to 4.2 deer/km² (T. Kautz, State University of New York College of Environmental Science and Forestry, pers. comm.). Potential neonate predators included coyotes, black bears, bobcats and wolves (Norton et al., 2018).

2.1.4 | North Carolina

In North Carolina, we conducted research on Fort Bragg Military Installation (hereafter, Fort Bragg; 35.1415°N, 79.0080°W) from 2011 to 2012. Fort Bragg was a 405 km² property owned by the U. S. Department of Defense and was located in the Sandhills physiographic region of central North Carolina. Lowland drainages with dense understorey were interspersed throughout the landscape. Deer density ranged from 2.0 to 4.0 deer/km² (Lashley et al., 2015). Neonate predators were coyotes and bobcats.

2.1.5 | South Carolina

In South Carolina, we conducted research on two study sites. We collected data at the Brosnan Forest (33.2146°N, 80.4479°W), a

58-km² tract in the Lower Coastal Plain in Dorchester County, South Carolina from 2006 to 2010. Brosnan Forest was mostly forested and vegetation was comprised of interspersed stands of mature longleaf pine, bottomland hardwood drains and mixed pine-hardwoods. Deer density was 20.0 deer/km² (Sullivan et al., 2018). Neonate predators included bobcats and coyotes.

The United States Department of Energy's Savannah River Site was a 780-km² National Environmental Research Park in the Upper Coastal Plain physiographic region of South Carolina. We collected data from the Savannah River study site (33.2464°N, 81.6679°W) from 2007 to 2012. Vegetation included upland and bottomland hardwoods (Kilgo et al., 2014). Deer densities ranged from 4.0 to 8.0 deer/km² (Kilgo et al., 2012). Neonate predators included coyotes and bobcats.

2.1.6 | Pennsylvania

We conducted research on two study sites in Pennsylvania. Penns Valley, an agricultural valley in Centre County is located about 30 km east of State College in Pennsylvania's Ridge-and-Valley physiographic province. We collected data from 2000 to 2001 from the Penns Valley study site (41.0221°N, 77.4358°W). Agricultural crops dominated the landscape. Small hardwood woodlots were located in agriculturally unproductive areas. Deer densities ranged from 12.3 to 13.5 deer/km² (C. Rosenberry, Pennsylvania Game Commission, pers. comm.).

The Quehanna Wild Area was a 200-km² site located in the Moshannon and Elk State Forests in Elk, Cameron and Clearfield counties in the Appalachian Plateau physiographic province. We collected data from 2000 to 2001 on the Quehanna Wild Area study site (41.2742°N, 78.2567°W). Forest cover was second- and third-growth mature hardwoods and regenerating stands including scattered herbaceous openings (Vreeland et al., 2004). Deer densities ranged from 11.9 to 14.2 deer/km² (C. Rosenberry, Pennsylvania Game Commission, pers. comm.). Neonate predators on the Penns Valley and the Quehanna Wild Area included coyotes, black bears and bobcats.

2.2 | Neonate capture and handling

We captured neonates with aid of vaginal implant transmitters (VITs; ~42%) or through opportunistic searches (~58%). For neonates captured with VITs, we used temperature-activated VITs (Models M3930, M3960B; Advanced Telemetry Systems) in which a change in temperature would activate a change in pulse frequency of the emitted signal. We followed implantation procedures described by Carstensen et al. (2003) and Bowman and Jacobson (1998). Depending on the study site, we monitored VITs once a week after implantation and increased monitoring intensity to once per day until the first birth of the season; we then monitored VITs at a 6- to 8-hr interval. We opportunistically searched for neonates from 10 April to 25 June, depending on mean birth dates on each respective study site. In addition

to foot searches to locate neonates (Vreeland et al., 2004), we used thermal-imaging cameras in South Carolina and Louisiana (Raytheon Palm IR 250D; McCoy et al., 2013; Shuman et al., 2017).

After detecting neonates, we captured them by hand or with dip nets. We blindfolded neonates and handled them wearing non-scented latex gloves. We minimized handling time to reduce stress and scent transfer (mean handling time <10 min) which likely minimized potential for marking-induced abandonment (Powell et al., 2005). We recorded sex and body mass from each neonate and at some study sites placed a unique identifier, usually a self-piercing ear tag (National Band and Tag Co.; model agpf#1, Allflex, TX; Original™ tags, Temple Tag Co.), in each ear. We used hoof growth to estimate birth date of neonates opportunistically captured at the Brosnan Forest, Escanaba and Crystal Falls study sites (Sams et al., 1996). We also estimated birth mass for fawns opportunistically captured at the Escanaba and Crystal Falls study sites using the methods described by Carstensen et al. (2009). Finally, we equipped each neonate with an expandable very high frequency collar (Models M4200, M4210; Advanced Telemetry Systems) designed to fall off between 6 and 9 months of age. We released neonates at the capture location. Each collar was equipped with a motion sensitive mortality switch set on a 4- or 8-hr delay.

2.3 | Neonate monitoring and fate determination

We monitored neonates to detect mortalities daily within the first 30 days of life (though we monitored neonates up to 5 days per week at the Escanaba study site). We then assigned cause of mortality based on field evidence at or near the collar or neonate remains. We examined carcasses for subcutaneous haemorrhaging beneath bite marks and investigated the trachea for signs of aspirated blood to determine whether predation was the cause of death or if scavenging had occurred. When we determined cause of death was predation, we identified predator species based on either field necropsies to measure bite patterns and haemorrhaging, or assessment of cache characteristics, size of the feeding area, consumption patterns and tracks or scat at the mortality site. We distinguished coyote and bobcat predation events based on trauma and condition of the remains. Caching behaviour is the most distinguishing aspect of bobcat predation events (Dill, 1947; Smith, 1945), whereas coyotes typically scatter remains and crush bones (White, 1973) or bury remains in mineral soil. Conversely, black bears rarely scatter remains and tend to have one relatively large feeding site where vegetation is matted down (Schlegel, 1976; Wade & Bowns, 1984). To confirm our field investigations at three study sites, we swabbed bite marks and sent samples to Wildlife Genetics International (WGI; Nelson, Canada) for DNA analysis of the saliva (Chitwood, et al., 2015; Kilgo et al., 2012; Shuman et al., 2017). When field evidence or DNA analysis could not indicate predator species, we listed the mortality cause as an unknown predator. We necropsied carcasses to determine cause of death for all non-predator related and some predator-related mortalities. Handling procedures were approved

under IACUC permit numbers A2012 06-006-Y3-A2, 120406-01, PRN 2008-1474, PRN 2004-0670, PRN 2007-1277, PRN 2008-1489, #09-004, #99R060, and 10-143-O. We also followed the American Society of Mammalogists guidelines for mammal care and use (Sikes & The Animal Care and Use Committee of the American Society of Mammalogists, 2016).

2.4 | Statistical analysis

We used a Cox proportional hazard model in the *SURVIVAL* package in Program R (version 3.4.3; R Core Team, 2017; Therneau, 2015) to assess what factors affected the 30-day neonate white-tailed deer survival. We assessed survival to 30 days because neonates are relatively immobile during this time period (Carl & Robbins, 1988; Lent, 1974) and most susceptible to predation (Grovenburg et al., 2011; Nelson & Woolf, 1987; Rohm et al., 2007). We accounted for variation among study areas by standardizing our fixed effects by study area. We calculated standardized birth date (\pm from median birth date) for each study area. We calculated standardized birth date from median birth dates to account for potential non-normal distributions of birth dates in some populations. We also calculated z-scores for body mass by study area. We included standardized birth date and its quadratic function as continuous variables to assess whether being born relatively early or late affected survival. We calculated the coefficient of variation (CV) of birth dates for each study area to assess if birth synchrony affected survival probability across populations. We included standardized birth date, its quadratic function and birth date CV as continuous variables and also included sex (categorical variable; Shuman et al., 2017) and birth mass z-score (continuous variable; Cook et al., 2004; Lomas & Bender, 2007; Shuman et al., 2017) in models to account for their potential impacts on survival. We refer to terms such as birth date and birth mass; however, capture date only was available for neonates obtained from the Quehanna Wild Area and Penns Valley study sites (~22% of neonates), birth date estimated from hoof growth was available for opportunistically captured neonates in the Brosnan Forest, Escanaba and Crystal Falls study sites (~35% of neonates) and all other study sites used VITs to capture neonates such that birth date was established from capture date (~42% of neonates). We also estimated birth mass from neonates opportunistically captured from the Escanaba and Crystal Falls study sites (about 14% of neonates), obtained capture mass from neonates opportunistically captured from the Brosnan Forest, Quehanna Wild Area and Penns Valley study sites (about 43% of neonates), and obtained birth mass from all neonates captured via VITs from all other study sites. Consequently, we used the established or estimated birth dates and birth mass when available, otherwise we interpreted capture date as birth date and capture mass as birth mass when no other data were available. We included latitude as a continuous variable to account for environmental variation among study sites. We only included mortalities associated with predation in our analyses. Because all predators were not present at each study site, we

assessed if the predator satiation and predator avoidance hypotheses were evident with four analytical scenarios: (1) combined all data and did not discriminate predator species, (2) restricted data to coyote and black bear predation events, (3) restricted data to only coyote predation events and (4) restricted data to only black bear predation events. Although we restricted data to analyse specific analytical scenarios, neonates were exposed to additional predator species in analytical scenarios 2, 3 and 4. We excluded entire study sites if a predator was not present (e.g. bears were not found at each study site). We considered hazard ratios important if their 95% confidence intervals (95% CIs) excluded 1, with hazard ratios >1 indicating the variable negatively affected neonate survival and hazard ratios <1 indicating the variable positively affected survival.

We then used a simple linear model to assess the relationship between latitude (explanatory variable) and birth date CV (response variable) to better understand if variation in climatic seasonality impacted birth synchrony. Finally, to test Sinclair et al. (2000) assumption that prey populations found at low population densities should display increased reproductive asynchrony, we used a simple linear

model to assess the relationship between birth season length and deer density (deer/km²). We considered latitude and deer density important if their 95% CIs excluded 0.

3 | RESULTS

We captured 1,032 neonates throughout our study. Median Julian birth date for all study sites ranged from 107.6 (~17 April, *SD* = 11.32, *n* = 210, Brosnan; Table 1) to 220.9 (~8 August, *SD* = 13.14, *n* = 51, Fort Rucker), and birth date CV ranged from 3.76 (Penns Valley) to 13.72 (Savannah River). Birth season length ranged from 35 days in Penns Valley and Quehanna Wild Area to 92 days in Savannah River (Table 1). Most study sites displayed synchronized birthing periods with ≥63% of births occurring ±7 days of median birthdate; however, there was substantial variation among study sites (Table 1). Predation was the primary cause of mortality (58.3%) but also varied among study sites (Table 2). Mean body mass was 3.56 kg (*SD* = 1.32, *n* = 370) and 3.73 kg (*SD* = 1.40, *n* = 492) for female and male neonates respectively.

TABLE 1 Birth season length (days) and percentage of births occurring ± 7 days of median birthdate for 1,032 neonate white-tailed deer captured in nine study sites across eastern North America from 2000 to 2014

Study site	Latitude and longitude	Birth season length (days)	Mean julian birth date	<i>SD</i>	<i>N</i>	Percentage of births occurring within 14 days
Fort Rucker	31.3437°N, 85.7080°W	52	220.9	13.1	51	45.1
Tensas	32.3176°N, 91.3771°W	57	196.9	12.0	56	37.5
Brosnan	33.2146°N, 80.4479°W	54	107.6	11.3	210	48.6
Savannah River	33.2464°N, 81.6679°W	92	137.8	18.9	216	29.6
Fort Bragg	35.1415°N, 79.0080°W	42	151.2	9.2	65	63.1
Penns Valley	41.0221°N, 77.4358°W	35	155.0	5.8	108	82.4
Quehanna Wild Area	41.2742°N, 78.2567°W	35	154.2	7.5	108	75.0
Escanaba	45.7452°N, 87.0646°W	40	152.7	6.5	141	78.0
Crystal Falls	46.0980°N, 88.3340°W	37	157.7	7.5	70	70.0

TABLE 2 Per cent total neonate mortality and associated per cent of mortalities attributed to predation, other natural, unknown or other causes for white-tailed deer neonates for their first 30 days of life captured in nine study sites across eastern North America from 2000 to 2014

Study site	Latitude and longitude	Per cent total neonate mortality	Mortality cause			
			Predation	Natural	Unknown	Other
Fort Rucker	31.3437°N, 85.7080°W	51.0	42.3	30.8	23.1	3.8
Tensas	32.3176°N, 91.3771°W	62.5	77.1	2.9	20.0	0.0
Brosnan	33.2146°N, 80.4479°W	17.1	19.4	41.7	38.9	0.0
Savannah River	33.2464°N, 81.6679°W	57.4	75.0	16.9	8.1	0.0
Fort Bragg	35.1415°N, 79.0080°W	73.8	47.9	35.4	12.5	2.1
Penns Valley	41.0221°N, 77.4358°W	22.2	20.8	45.8	33.3	0.0
Quehanna Wild Area	41.2742°N, 78.2567°W	31.5	64.7	20.6	14.7	0.0
Escanaba	45.7452°N, 87.0646°W	28.7	53.7	19.5	22.0	4.9
Crystal Falls	46.0980°N, 88.3340°W	44.0	78.0	12.5	2.5	7.5

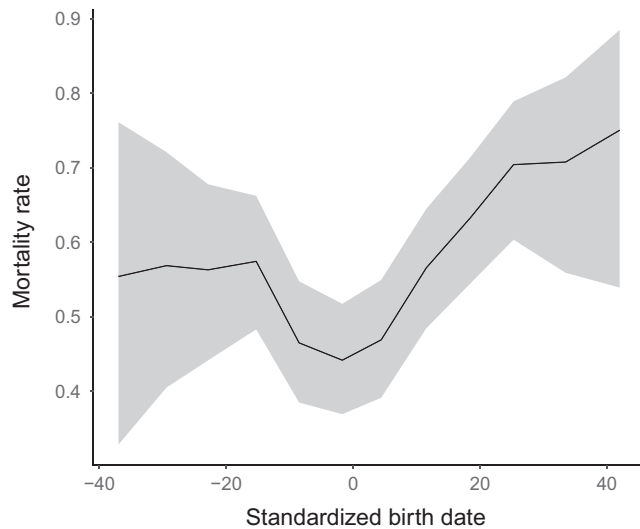


FIGURE 3 Predation mortality hazard by standardized birth date for 165 neonates depredated by coyotes from nine study sites across eastern North America from 2000 to 2014. Individual neonates born after their standardized birth date experienced increased mortality

We included 867 neonates in analyses after excluding those dying from causes other than predation. Coyotes were the main source of predation across study sites ($n = 165$), followed by bobcats ($n = 32$), black bears ($n = 29$) and wolves ($n = 3$; see Table S1 in Supporting Information). Mean age of neonates when predation occurred ranged from 8.7 days for neonates depredated by wolves to 13.0 days for those depredated by coyotes. We noted that 79% of mortality events attributed to black bears occurred within the first 14 days of life, whereas nearly half of all mortalities attributable to coyotes occurred after day 14 (see Table S2 in Supporting Information).

The relationship between relative birth timing and neonate survival differed among analytical scenarios. We documented a weak effect of relative birth date on mortality in the coyote only scenario (analytical scenario 3; hazard ratio = 1.012, 95% CI = 1.000–1.025; Figure 3), although its quadratic function was not important (95% CIs included 1). Birth date CV was negatively associated with neonate survival for all analytical scenarios except when all predators were included in the analysis (analytical scenario 1; hazard ratio range: 1.067–6.481, 95% CIs excluded 1; Table 3; Figure 4),

Predator composition	Variable	Hazard function	Lower 95% CI	Upper 95% CI
All Predators	Standardized birth date ^a	1.008	0.997	1.018
	Standardized birth date ^{2b}	1.000	0.999	1.000
	Birth date CV ^c	1.045	0.991	1.102
	Birth mass ^d	0.842	0.735	0.965
	Neonate sex	0.953	0.739	1.227
	Latitude	0.966	0.928	1.006
Coyotes and Bears	Standardized birth date ^a	1.010	0.999	1.022
	Standardized birth date ^{2b}	1.000	0.999	1.001
	Birth date CV ^c	1.067	1.004	1.133
	Birth mass ^d	0.872	0.748	1.017
	Neonate sex	0.936	0.700	1.251
	Latitude	0.950	0.904	0.997
Coyotes	Standardized birth date ^a	1.012	1.000	1.025
	Standardized birth date ^{2b}	1.000	0.999	1.000
	Birth date CV ^c	1.139	1.063	1.220
	Birth mass ^d	0.909	0.771	1.070
	Neonate sex	0.881	0.643	1.207
	Latitude	0.959	0.904	1.017
Bears	Standardized birth date ^a	1.004	0.962	1.049
	Standardized birth date ^{2b}	0.999	0.997	1.002
	Birth date CV ^c	6.481	1.733	24.238
	Birth mass ^d	0.628	0.390	1.010
	Neonate sex	1.040	0.482	2.248
	Latitude	1.050	0.885	1.246

^aBirth date standardized relative to study site.

^bStandardized birth date quadratic function.

^cBirth date CV calculated by study site to represent variation in birth synchrony across study sites.

^dZ-scores calculated by study site.

TABLE 3 Model results for 867 white-tailed deer neonates captured at nine study sites in eastern North America from 2000 to 2014. We assessed how standardized birth date and its quadratic function, birth date coefficient of variation, birth mass, sex and latitude affected white-tailed deer neonate 30-day survival. Hazard ratios > 1 indicate the variable negatively affected neonate survival, whereas hazard ratios < 1 indicate the variable positively affected survival

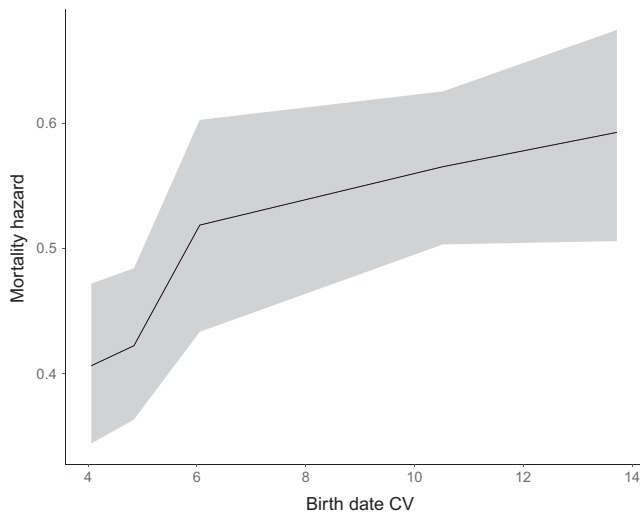


FIGURE 4 Coyote *Canis latrans* and black bear *Ursus americanus* predation mortality hazard by the coefficient of variation for birth date for 788 neonates captured from nine study sites across eastern North America from 2000 to 2014. Asynchronous populations experienced increased depredation

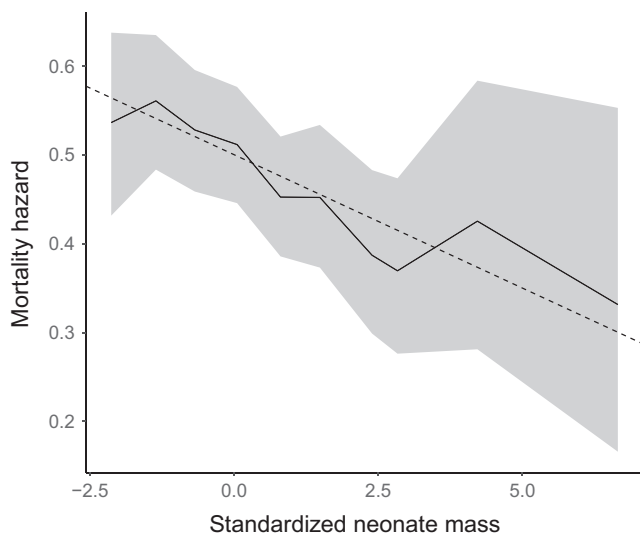


FIGURE 5 Predation mortality hazard by standardized neonate mass for 867 neonates captured from nine study sites across eastern North America from 2000 to 2014. Dashed line represents a perfectly linear relationship

indicating neonates found in asynchronous populations were at greater mortality risk than those found in synchronous populations. Standardized neonate body mass was positively associated with survival (hazard ratio = 0.842, 95% CI = 0.735–0.965; Figure 5), with heavier neonates displaying decreased risk; however, this relationship was only important when we assessed survival probability with all predators (analytical scenario 1). Sex was not related to survival for any analytical scenario (95% CIs included 1). Latitude was only important in the coyotes and bears only scenario (analytical scenario 2; hazard ratio = 0.950, 95% CI = 0.904–0.997) such that the hazard of neonates to bears and coyotes on sites where those

predators occurred varied predictably with latitude. Overall, we were able to fit a model for each analytical scenario (likelihood ratio test; $p < 0.001$). Models moderately predicted survival when using data from black bear predation events only (analytical scenario 4; $R^2 = 0.64$); however, model performance was less for all other analytical scenarios ($R^2 \leq 0.24$).

Opportunistically captured neonates are on average about 3.5 days older than their counterparts captured via VITs (Grovenburg et al., 2012; Kautz et al., 2019). Additionally, including neonates opportunistically captured after their birth date can affect results from survival analyses (Chitwood et al., 2017; Gilbert et al., 2014). Therefore, given we included both opportunistically captured neonates (potentially captured days after their birth date) and neonates captured via VITs, we conducted a separate analysis using only neonates captured via VITs and present those results in Table S3 in Supporting Information.

Finally, latitude affected birth date CV ($\beta = -0.539$, 95% CI = -0.571 to -0.507) such that study sites at lower latitudes were more asynchronous than study sites at higher latitudes ($R^2 = 0.56$). There was no relationship between deer density and reproductive synchrony ($\beta = -0.077$, 95% CI = -2.975 to 2.822 , $R^2 = 0.00$).

4 | DISCUSSION

Species with nonprecocial young that display a 'hider' strategy early in life are predicted to display asynchronous birth seasons to avoid predators (predator avoidance hypothesis; Sinclair et al., 2000). However, using white-tailed deer as a model species, our results do not support the predator avoidance hypothesis as neonates were generally at increased predation risk with increasing birth asynchrony. Sinclair et al. (2000) also suggested ungulate species that occur at low densities that cannot satiate predators should display asynchronous birthing seasons; however, our results do not support this either, as we detected no relationship between deer density and reproductive synchrony. Additionally, given environmental conditions affect birth synchrony, birth asynchrony may only be a viable predator defense strategy for ungulates at tropical latitudes (African ruminants; reviewed in Zerbe et al., 2012). Therefore, the predator avoidance hypothesis may not be applicable to ungulate species occurring at temperate latitudes.

We provide partial support for the predator satiation hypothesis (Darling, 1938) as neonates born after, but not before, peak parturition were at increased risk of predation by coyotes. Although data collected from several species provides evidence for the predator satiation hypothesis (wildebeest *Connochaetes taurinus*, Estes & Estes, 1979; snowshoe hares *Lepus americanus*, O'Donoghue & Boutin, 1995; roe deer, Panzacchi et al., 2008), data collected from some species of large ungulates do not (caribou *R. tarandus*, Post et al., 2003; moose *Alces alces*, Bowyer et al., 1998), even though they may display synchronous birth dates. Regardless, we detected partial support for the predator satiation hypothesis in the coyote only analytical scenario. Although white-tailed deer neonates

follow a general trend of decreased survival before and after peak parturition, we only detected a weak relationship between standardized birth date, but not the quadratic function, and neonate survival in the coyote only analytical scenario. However, the relationship between standardized birth date and neonate survival may be related to relatively few mortalities occurring at the earliest part of the parturition season. Although speculative, coyote density may also be a factor as a high density of coyotes may induce increased birth synchrony leading to predator satiation; however, we did not have data on coyote density to further investigate this relationship. Regardless, our results support Kilgo et al. (2012) and Kilgo et al. (2014) who determined survival probability decreased for late-born white-tailed deer neonates in South Carolina (USA) where coyotes were the main predators. Coyotes which were present at each of our study sites, are considered a generalist predator (Boutin & Cluff, 1989; Gese et al., 1988), rely greatly on mammalian prey (Ward et al., 2018) and display the ability to switch prey when new prey items become available (Patterson et al., 1998; Petroelje et al., 2014). At local scales, coyotes can have population-level impacts on survival of white-tailed deer (neonate survival $\leq 18.5\%$, Chitwood, et al., 2015; declining white-tailed deer population trajectory [$\lambda = 0.905$], Chitwood et al., 2015). Given predation can act as a selective pressure to stabilize birth synchrony (Jarnemo et al., 2004; Testa, 2002), we hypothesize coyote predation could be a selective pressure great enough to increase reproductive synchrony such that predator satiation may become a feasible defense strategy for neonates at local spatial scales.

We determined that birthing seasons became more asynchronous with decreased climatic seasonality, which is consistent with other literature. For instance, Rutberg (1987) conducted a literature review of 27 ruminant species and determined climatic seasonality and resource availability accounted for almost half the variance of birth-season length. English et al. (2012) performed an updated analysis of this concept and showed similar results; birth-season length was also influenced by seasonality and resource availability. These results are supported by Post et al. (2003) who determined that caribou calving season in West Greenland was highly synchronized even in the absence of predators and was related to the progression of plant phenology. Similarly, Bowyer et al. (1998) hypothesized climatic variability, and not predation risk, likely affected birth-season length for moose in Alaska, USA. Although our results show white-tailed deer display variation in the degree of birth synchrony across their range, all of our study populations experienced some degree of climatic variability and resource limitation with populations at northern latitudes experiencing greatest variability (Hewitt, 2011). Subsequently, asynchronous populations were associated with decreased climatic seasonality. Breeding date synchrony for white-tailed deer may therefore be regulated more by climatic variability and resource limitation than predation risk.

Predators were responsible for most mortalities in our study, suggesting they are capitalizing on the resource pulse (an event of large magnitude that occurs over a short period of time; Yang et al., 2008)

neonates represent on the landscape (Petroelje et al., 2014). Brose et al. (2008) suggested that as predator size increases, the ability to efficiently capture prey decreases with age and mobility of the prey. Although neonates are generally mobile after 30 days of age (Carl & Robbins, 1988; Lent, 1974; Vreeland et al., 2004), their degree of mobility increases up to 30 days, making successful predation more difficult and less energetically rewarding for large predators. Temporal variation in predation on white-tailed deer neonates has subsequently been reported (Nelson & Woolf, 1987; Petroelje et al., 2014; Shuman et al., 2017). Therefore, temporal use of white-tailed deer neonates likely varies by predator, causing white-tailed deer neonates to be at prolonged mortality risk in multiple-predator systems.

We determined that heavier neonates displayed a decreased predation risk throughout their first 30 days of life, consistent with previous studies (Carstensen et al., 2009; Kunkel & Mech, 1994), although some studies have failed to observe this relationship (Grovenburg et al., 2011; Kilgo et al., 2012; Rohm et al., 2007). However, this result may have been biased given we obtained or estimated birth mass in six study sites, whereas we obtained capture mass only from three study sites and subsequently was used in our analyses. Interestingly, birth mass was only important in all predator scenarios (scenario 1) and if a bias occurred, the relationship between birth mass and neonate survival may have been more consistent across analytical scenarios. Regardless, heavier offspring may have greater survival if body mass is related to growth rate, which has been reported for amphibians (Altwegg & Reyer, 2003; Cabrera-Guzmán et al., 2013; Goater, 1994) where heavy individuals grow at an increased rate and display increased survival compared to their lighter conspecifics. Although this same relationship between growth rate and survival has not been reported for white-tailed deer neonates, there is indirect evidence. For example, heavier ungulate neonates display increased growth rates compared to lighter neonates (Gaillard et al., 1997; Verme, 1989). Furthermore, Michel et al. (2018) found connectivity of hiding cover positively affected white-tailed deer neonate survival in grassland ecosystems after, but not before they became mobile. Therefore, heavier white-tailed deer neonates may grow at an increased rate, become mobile earlier in life, and display increased survival because of their ability to evade predators by fleeing to high-quality escape cover compared to lighter counterparts.

5 | CONCLUSIONS

We did not find support for the predator avoidance hypothesis, as we detected consistent negative effects of birth asynchrony on survival. However, although white-tailed deer neonates do not fit the criteria (precocial young exposed to specialist predators), our results partially support the predator satiation hypothesis, as late-born neonates were at greater predation risk than neonates born before and during peak parturition season. Furthermore, we documented that climatic seasonality affects reproductive synchrony in white-tailed

deer, as asynchronous populations were associated with decreased climatic seasonality. Although climatic seasonality likely affects birth phenology and synchrony, some predators (coyotes) may also exhibit a directional selective pressure great enough to cause a shift in birth dates as survival probability decreased with increased asynchrony thereby making predator satiation a more efficient predator defense strategy in local populations that are currently asynchronous. However, continuous monitoring of birth dates is needed to verify this phenological response to predation. Regardless, the combination of birth phenology, birth synchrony and predator composition likely affects white-tailed deer neonate survival in eastern North America.

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CONFLICT OF INTEREST

Authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

All authors contributed equally to this manuscript.

DATA AVAILABILITY STATEMENT

Data are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.pg4f4qrmn> (Michel et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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