White-tailed deer neonate survival in the absence of predators

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Abstract. Several factors influence neonate survival rates in white-tailed deer (Odocoileus virginianus), and an emphasis on predation as the primary limiting factor to neonate recruitment may serve to detract researchers from understanding other influential variables. We estimated survival and cause-specific mortality of white-tailed deer neonates in the absence of predators with an emphasis on assessing how birth mass, dam maturity, and weather covariates affect neonate survival. Additionally, we examined the influence of capture method (opportunistic searches vs. vaginal implant transmitter; VIT) on survival estimates. We captured 109 neonates using opportunistic capture (n = 55) and VITs (n = 54) in Sussex County, Delaware, USA, during 2016 and 2017. There are no established predator populations (i.e., black bear, bobcat, and coyote) within the study area. We observed greater 90-d survival rates in opportunistically captured neonates (0.69, 95% CI = 0.55–0.87) compared to VIT-captured neonates (0.44, 95% CI = 0.34–0.61), a difference driven by inobservance of early-life mortality events among neonates captured opportunistically. Natural causes excluding predation (e.g., disease, emaciation, and birth defects) accounted for all observed mortality (n = 42). Mortality related to disease, emaciation, and birth defects typically occurred in the first 7 d of life and was underrepresented in the opportunistically captured sample. Birth mass, dam age class, and precipitation influenced neonate mortality risk within the first 7 d of life, but no variables were associated with survival from 8 to 28 d of life. Non-predation-related mortality causes in our study area resulted in survival rates comparable to regions with established predator communities. Non-predation-related mortality may be the ultimate driving factor controlling neonatal survival in other regions but can be obfuscated by more proximal mortality sources, such as predation.

Key words: compensatory mortality; neonate; Odocoileus virginianus; predation; survival; white-tailed deer.

INTRODUCTION

Population dynamics of large herbivores are primarily driven by rates of adult female survival and juvenile recruitment (Gaillard et al. 2000, Chitwood et al. 2015a). Because adult female survival is generally high and constant relative to juvenile recruitment (Gaillard et al. 1998), biologists attempting to increase population growth rate often focus management efforts on increasing neonate survival (Linnell et al. 1995, Chitwood et al. 2017). In white-tailed deer (Odocoileus virginianus; hereafter deer) populations, estimates of neonate survival and cause-specific mortality vary regionally (Gingery et al. 2018), the influence of additive and compensatory mortality sources is not well understood, and the results of management practices targeted at
increasing neonate survival have been mixed (Kilgo et al. 2014, Gulsby et al. 2015).

Recent studies across North America have documented neonatal survival estimates for deer populations ranging from 14% in North Carolina (Chitwood et al. 2015b) to 87% in Minnesota (Grovenburg et al. 2011), with many studies listing predation as the leading cause of mortality (Vreeland et al. 2004, Kilgo et al. 2012, Shuman et al. 2017, Kautz et al. 2019). Although coyote (Canis latrans) are typically the predominant predator of deer neonates, bobcat (Lynx rufus) and black bear (Ursus americanus) are also common predators (Gingery et al. 2018). Whether predation on neonatal deer is an ultimate or proximate cause of mortality is an important but poorly understood aspect of deer population dynamics. Determining the ultimate cause of mortality is inherently difficult because researchers typically collect detailed animal condition data at only two time points during the study: capture and mortality. The resulting data gap leaves researchers to speculate as to the condition of the animal, the events leading up to mortality, and to determine the causation based solely on the information available at the time of mortality (Chitwood et al. 2014, 2017). The frequent inclusion of opportunistically captured animals (Grovenburg et al. 2011, Duquette et al. 2014, Warbington et al. 2017, Wright et al. 2019) further complicates cause-specific mortality studies. Opportunistic capture involves observing maternal behavior or searching fawning habitat to encounter neonates (Huegel et al. 1985, Ditchkoff et al., 2005, Haskell et al. 2007). Opportunistic capture methods can lead to biased survival estimates due to inaccurate age estimation and failure to observe mortalities that occur in the first days after birth (Ozoga and Rodney 1988, Haskell et al. 2007, Gilbert et al. 2014, Chitwood et al. 2017).

Many recent studies have investigated the impact of predation on neonatal mortality rates (Kilgo et al. 2012, Nelson et al. 2015, Kautz et al. 2019), but other factors influencing survival generally receive considerably less attention (Gingery et al. 2018, Michel et al. 2018). Birth mass is positively associated with survival probability in neonates (Linnell et al. 1995, Saalfeld and Ditchkoff 2007, McCoy et al. 2013), but a paucity of literature explores other maternal influences. Neonates born from mature dams may have a reduced mortality risk relative to those of younger dams due to both maternal experience and the propensity for older, more dominant females to occupy and defend better quality habitats (Townsend and Bailey 1981, Ozoga and Verme 1986, Blank 2019). Weather conditions may also affect neonate survival rates. The influence of daily weather has been documented in other species such as wild turkey (Meleagris gallopavo), where poult survival is negatively related to precipitation (Vangilder and Kurzejeski 1995, Roberts and Porter 1998). Precipitation and minimum temperature are reported to influence neonatal survival at multiple spatial and temporal scales, but with conflicting results (Ginnett and Young 2000, Warbington et al. 2017, Michel et al. 2018).

Managers of white-tailed deer require a better understanding of factors other than, or in addition to, predation that influence neonatal survival. Predator-related mortality is observed more frequently than other mortality sources (Chitwood et al. 2017, Gingery et al. 2018), but predation may be either nonadditive or the proximate cause of mortality. We examined neonate survival in a region where natural predators of white-tailed deer neonates were either completely absent or functionally absent from the landscape. Our objectives were to (1) estimate survival of white-tailed deer neonates in the absence of natural 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 mass, dam maturity, and weather covariates influence neonate survival. We predicted that neonate survival in the absence of natural predators would be greater than survival rates reported from regions with established predator communities (Shuman et al. 2017, Warbington et al. 2017, Wright et al. 2019) and that low birth mass, greater daily precipitation, low daily temperature, and being born to a young female would be associated with an increased daily morality risk (Verme 1989, Michel et al. 2018). Furthermore, we hypothesized that neonates captured via opportunistic methods would demonstrate inflated survival estimates relative to neonates captured at the birth site using VITs (Gilbert et al. 2014, Chitwood et al. 2017).
METHODS

Site description

We conducted our research on a mixture of public and private properties in Sussex County, Delaware (2420 km²; Fig. 1). Bordering Sussex County to the east was the Atlantic Ocean, to the north was Kent County, Delaware, and to the south and west was Maryland. Agriculture (41%), upland forest (22%), forested wetland (22%), and development (15%) were the primary land uses, and major agricultural crops included corn, soybeans, and winter wheat (National Agricultural Statistical Service 2012). Deer density in Sussex County was approximately 19 deer/km², and there were no established deer predator communities aside from humans (Delaware Division of Fish and Wildlife 2010). Confirmed sightings of coyote in Sussex County are infrequent. The state opened a hunting and trapping season in 2014, and according to mandatory reporting data, no coyotes were harvested in Sussex County during either 2016 or 2017 (C. Baird, unpublished data). No confirmed black bear or bobcat sightings have occurred in Sussex County for >100 yr. The only established natural carnivore potentially large enough to prey upon neonates was red fox (Vulpes vulpes), although we are not aware of any documented case of a white-tailed deer neonate ever being successfully depredated by a red fox, and foxes are typically not considered predators of neonate deer in North America (Ozoga and Verme 1982, Linnell et al. 1995). While domestic dogs (Canis lupus familiaris) are capable of occasionally depredating neonates, they are not considered a major predator in the region (Vreeland et al. 2004).

Mean annual precipitation during the study was 127 cm, comparable to the 30-yr (1981–2010) mean of 119 cm. Temperatures during the study (2015–2017) ranged from −14°C to 36°C (National Climatic Data Center 2019) and did not differ from the long-term averages. Spring and summer precipitation averaged 78 cm, with temperatures ranging from 2°C to 36°C (National Climatic Data Center 2019).

Predator surveys

We conducted predator camera surveys from December to March during 2016 and 2017. We deployed 23 cameras (Hyperfire HC600, Reconyx; Holmen, Wisconsin, USA) across each study property where we captured adult females and limited placement to ≤3 cameras per property. The largest property accessed in the study was 298 ha, resulting in a minimum camera density of 1 camera/100 ha on study properties. We set camera traps over scent stations that utilized predator baits and scent lures to increase the probability of capturing any predator or mesocarnivores in the area. We refreshed baits and scents every 2 weeks (Gompper et al. 2006, Kelly and Holub 2008). We also employed passive camera sets, which we placed in high wildlife traffic areas (e.g., field edges, game/hiking trails, and travel corridors). To cover as much of the properties as possible, we placed cameras a minimum of 200 m apart. We secured cameras 30–40 cm off the ground, allowing the capture of smaller mesocarnivores, such as raccoons (Procyon lotor) and red fox while still capturing larger animals (Gompper et al. 2006).

Adult deer capture and VIT monitoring

We captured adult female white-tailed deer from December to April of 2015–2017 using rocket nets, drop nets, and clover traps baited with whole kernel corn (Schemnitz et al. 2012). We followed procedures outlined in Haus et al. (2019) for animal capture, immobilization, and handling. We aged deer using tooth replacement and wear (Severinghaus 1949) and fitted all females ≥1.5 yr of age with radio collars and vaginal implant transmitters (VITs) from Advanced Telemetry Systems (Isanti, Minnesota, USA). We deployed GPS collars (model G2110E2, 800 g) with VITs (model M3930U, 23 g) on 44 females and VHF collars (model M2230B, 190 g) with VITs (model M3930, 22 g) on an additional eight females. We followed established guidelines for VIT deployment (Bowman and Jacobson 1998, Carstensen et al. 2003) and inserted transmitters to a depth of 20 cm. We monitored animal condition and vital signs (temperature, heart rate, and respiration) until individuals left the capture site under their own power.

Adult and VIT monitoring

We determined the location of VHF-collared females and monitored VIT status once/week following deployment until 1 May. Starting 1 May,
we increased the frequency of relocation and VIT status monitoring attempts for VHF-collared females to every 6 h to ensure timely notification of a birth event (Saalfeld and Ditchkoff 2007, Kilgo et al. 2012, Jackson and Ditchkoff 2013). We received remote notifications for GPS-collared females including fix locations and VIT status daily until 1 May. Following 1 May, we received GPS locations and VIT status reports every hour.

**Neonate capture**

We began searching for the birth site 1–2 h after we received notification of a VIT expulsion using the VHF signal emitted by the VIT. If we discovered the VIT outside of an apparent birth site, we marked the location with flagging tape and searched the area until we found a birth site. Following discovery of the birth site, we initiated the search for the neonates. If we did not locate any neonates in the immediate vicinity of the birth site, we systematically searched the surrounding area until we found $\geq 1$ neonate. We used a thermal imaging camera (Scout III, FLIR Systems; Wilsonville, Oregon, USA) to aid in both diurnal and nocturnal searches (Saalfeld and Ditchkoff 2007, Kilgo et al. 2012, Jackson and Ditchkoff 2013). Throughout the season, we opportunistically captured neonates found during daily activities (e.g., telemetry, vegetation measurements, and mortality investigations) and nocturnal searches. For nocturnal searches, we systematically searched fawning habitat using thermal scopes and spotlights to locate hiding neonates.

Once located, we blindfolded neonates and moved them to a handling location away from their birth site or bed sites to minimize human scent. We wore non-scented latex gloves when handling the neonates to prevent the transfer of human oils and scent (Kilgo et al. 2012). We estimated age of neonates captured opportunistically using a combination of behavior, hoof development, and umbilicus condition (Sams et al. 1996, Haskell et al. 2007). To measure birth mass (or mass at time of capture for opportunistically captured neonates), we placed neonates in cotton pillowcases attached to a scale. Once weighed, we fitted each neonate with an expandable VHF collar with a 2-h mortality sensor (model M4210, 63 g; Advanced Telemetry Systems, Isanti, Minnesota, USA). Each neonate received two self-piercing, numbered metal ear tags (model 1005-49, National Band and Tag...
Company, Newport, Kentucky, USA) and two white, plastic button cattle tags (3 cm diameter) with black numbers (Allflex USA, Dallas, Texas, USA). Following handling, we returned neonates to the birth site or bed site and left the area as quickly as possible. We followed the American Society of Mammologists guidelines for mammal care and use (Sikes 2016), and the University of Delaware Institutional Animal Care and Use Committee approved all handling protocols for adult females and neonates (protocol 1288).

**Survival rates and cause-specific mortality**

We located neonates on an age-based schedule. For the first 28 d, we located individuals every 12 h to ensure timely notification of mortality status during the period of greatest risk for neonates (Linnell et al. 1995, Saalfeld and Ditchkoff 2007). We continued to monitor individuals every 24 h from 29 to 60 d old, three times per week from 61 to 90 d old, and once per week thereafter until the collar failed or a mortality event occurred. Upon the detection of a mortality signal, we tracked the signal to the carcass, examined the remains, and recorded photographs and descriptions of the mortality site. If the viscera were intact (i.e., limited scavenging), we collected the carcass and submitted it for gross necropsy and histology to the Pennsylvania Animal Diagnostic Laboratory (PADL) at the University of Pennsylvania.

We estimated neonatal survival at 7, 28, and 90 d postpartum using a Kaplan-Meier survival function in the survival package of program R (Kaplan and Meier 1958, Therneau 2015). We used the day of birth as the entry time (day 0) for all neonates captured using VITs and a staggered-entry design to incorporate neonates captured opportunistically (Pollock et al. 1989). We compared survival between sexes, years, and capture methods using a log-rank test. We determined cause of mortality by reviewing PADL necropsy and histology reports and from notes and photographic observations from the field, and we categorized mortalities as predation, natural mortality not related to predation, or unknown. We defined natural mortality to include all nonhuman- and non-predator-induced deaths (e.g., disease, birth defect, and emaciation). We requested the PADL staff to document any potential indication of predation (e.g., puncture wounds with subcutaneous hemorrhaging, aspirated blood in the trachea, external bleeding, size, and location of tooth marks). Unknown mortalities included all cases in which the specific cause of death could not be determined.

**Survival modeling**

We used Cox proportional hazard models (Cox 1972) with an age-based timescale (Fieberg and DelGiudice 2009) to determine the impact of specific covariates on neonatal survival during two distinct periods corresponding to the preponderance of mortality in neonates (Rohm et al. 2007, Carstensen et al. 2009): 0–7 and 8–28 d postpartum. Because we observed few mortalities beyond 28 d (n = 9), we did not model the impact of covariates during the 29- to 90-day period. We included only neonates captured at birth sites using VITs because we were unable to link opportunistically captured neonates to their dams or accurately estimate birth mass.

We developed 14 a priori candidate models for each survival period, which included covariates for birth mass, dam maturity, daily precipitation, and minimum temperature. We used dam maturity to explore the influence of maternal experience and social dominance on neonatal survival (Piccolo et al. 2010). We designated females ≥4 yr of age at the time of parturition as mature and females <4 as immature (Kunkel and Mech 1994). Ozoga and Verme (1986) reported improvements in maternal behavior as females aged, and females approach peak body mass at approximately 4 yr of age (Strickland and Demarais 2000, Jones et al. 2010, Ditchkoff 2011). Although accurately aging deer to the year using tooth replacement and wear methodology has been criticized for deer ≥2 yr old (Storm et al. 2014), 70–80% of replacement and wear estimates match cementum annuli estimates when pooling age classes such as 1.5–2.5 yr old vs. ≥3.5 yr old at the time of capture (Storm et al. 2014, Adams 2019). We included weather covariates for total daily precipitation and daily minimum temperature, as these variables potentially influence neonatal survival (Ginnett and Young 2000, Warbington et al. 2017, Michel et al. 2018). Because the influence of birth mass on neonate survival is well documented (Linnell et al. 1995,
Saalfeld and Ditchkoff 2007, McCoy et al. 2013), we included models with birth mass as a main effect and interaction terms with all other variables. We checked all models to ensure the assumption of proportionality among hazard rates was satisfied (Grambsch and Therneau 1994). Using Akaike’s information criterion corrected for small sample size ($\Delta AIC_c$) values, we compared the candidate models to identify influential covariates that explained the greatest amount of variation in neonate survival. We used the number of mortality events as the sample size for calculation of $AIC_c$ values. We considered the models with the lowest $AIC_c$ value to have more support and be more parsimonious than models with $\Delta_0 AIC_c$ ($\Delta_0 AIC_c = AIC_{c,i} - AIC_{c,min}) \geq 2$ (Hurvich and Tsai 1989, Burnham and Anderson 2002, Posada and Buckley 2004). We evaluated the importance of individual variables within models using the 95% confidence interval of the hazard ratio ($exp[\beta]$). Hazard ratios with 95% confidence interval overlapping 1 indicated the variable did not influence risk of mortality.

**RESULTS**

Camera surveys for predators resulted in 9,379 photographs over 1,186 trap nights. We observed 0 detections of coyote, bobcat, or black bear during both 2016 and 2017. We observed six unique detections of domestic dogs, two of which were captured via VIT (0.70, 95% CI 0.67–1.00) relative to neonates captured using VIT ($\chi^2 = 17.40, P = 0.001$; Fig. 3). The estimated survival rate at 7 d postpartum was 12% greater for opportunistically captured neonates (0.82, 95% CI = 0.67–1.00) relative to neonates captured via VIT (0.70, 95% CI = 0.59–0.84). The difference increased to 23% by 28 d postpartum (0.76, 95% CI = 0.61–0.94; and 0.53, 95% CI = 0.41–0.68 for opportunistic and VIT captures, respectively). After 28 d, capture method did not appear to influence survival estimates, and the 90-d survival rate was 25% greater in opportunistically captured neonates (0.69, 95% CI = 0.55–0.87; and 0.44, 95% CI = 0.34–0.61 for opportunistic and VIT captures, respectively). Survival to 90 d was 0.53 (95% CI = 0.44–0.65) when combining opportunistic and VIT-captured neonates using a staggered-entry design (Fig. 2), which is 9% greater than estimates using only VIT-captured neonates.

The leading cause of mortality was emaciation (50% of mortalities; $n$ = 21) for both opportunistic and VIT-captured neonates. Milk was present in the stomach in 62% ($n$ = 13) of the cases where emaciation was a contributing factor to mortality. Disease (21% of mortalities; $n$ = 9) was a

**Survival and cause-specific mortality**

We observed 42 mortalities within 90 da of birth, all of which we classified as natural mortality not related to predation (Table 1). We did not document any human-induced mortalities (e.g., vehicle collisions or agricultural equipment). Survival rates during the three periods (0–7, 8–28, and >28 d postpartum) appeared to be typified by different curve types (Demetrius 1978; Fig. 2). The 0- to 7-d period consisted of high rates of early mortality occurring over a relatively small time period typical of a type III survival curve and accounted for nearly half (48%; $n$ = 20) of all mortalities. The slope of the survival curve appeared to decrease and more closely resembled a linear type II curve during the 8- to 28-d period, which accounted for 31% ($n$ = 13) of all mortalities. Survival rate beyond 28 d postpartum plateaued, with only 21% ($n$ = 9) of mortalities occurring over a 62-d period (29–90 d).

We did not find evidence to support a difference in the overall 90-d Kaplan-Meier survival curves between years ($\chi^2 = 0.60$, $P = 0.44$) or between sexes ($\chi^2 = 0.70$, $P = 0.42$), so we pooled data for neonate survival across levels for both year and sex. Survival differed between capture method ($\chi^2 = 14.70, P < 0.001$; Fig. 3). The estimated survival rate at 7 d postpartum was 12% greater for opportunistically captured neonates (0.82, 95% CI = 0.67–1.00) relative to neonates captured via VIT (0.70, 95% CI = 0.59–0.84). The difference increased to 23% by 28 d postpartum (0.76, 95% CI = 0.61–0.94; and 0.53, 95% CI = 0.41–0.68 for opportunistic and VIT captures, respectively). After 28 d, capture method did not appear to influence survival estimates, and the 90-d survival rate was 25% greater in opportunistically captured neonates (0.69, 95% CI = 0.55–0.87; and 0.44, 95% CI = 0.34–0.61 for opportunistic and VIT captures, respectively). Survival to 90 d was 0.53 (95% CI = 0.44–0.65) when combining opportunistic and VIT-captured neonates using a staggered-entry design (Fig. 2), which is 9% greater than estimates using only VIT-captured neonates.

The leading cause of mortality was emaciation (50% of mortalities; $n$ = 21) for both opportunistic and VIT-captured neonates. Milk was present in the stomach in 62% ($n$ = 13) of the cases where emaciation was a contributing factor to mortality. Disease (21% of mortalities; $n$ = 9) was a
substantial cause of natural mortality for neonates in our study and included bacterial infections (pleuropneumonia and sepsis, $n = 7$), ischemic hepatic necrosis ($n = 1$), and focal necrotizing encephalitis ($n = 1$). Histological analysis identified *Theileria cervi* infection as the cause of death for one neonate but was present and may have contributed to mortality in five additional animals. We observed nine mortalities in which the cause of death could not be determined; either the necropsy results reported no abnormalities ($n = 2$) or the carcass was too...
heavily scavenged by turkey vultures (*Cathartes aura*) or black vultures (*Coragyps atratus*) to submit for testing (*n* = 7). No signs of predation were apparent at the mortality site or upon necropsy for any neonate with an unknown mortality cause (Table 1).

**Survival modeling**

After checking for derivations in proportionality, we observed no violations in assumptions for any model. For the 0- to 7-d period, three competing Cox proportional hazard models accounted for 80% of the model weight and included covariates for birth mass, daily precipitation, and dam maturity (Table 2). Birth mass appeared in all three competing models. The univariate model for birth mass (exp[β] = 0.10; 95% CI = 0.04–0.29) predicted that for every 1 kg increase in a neonate’s birth mass, instantaneous risk of mortality was reduced by 90%. The model including birth mass (exp[β] = 0.12; 95% CI = 0.04–0.32) and precipitation (exp[β] = 1.62; 95% CI = 1.08–2.43) predicted a 62% increase in the instantaneous risk of mortality for every 1 cm increase in daily precipitation for neonates at mean birth mass (2.9 kg). The model of birth mass (exp[β] = 0.11; 95% CI = 0.04–0.31) and dam maturity (exp[β] = 0.33; 95% CI = 0.07–0.89) predicted a 67% decrease in the instantaneous risk of mortality for neonates of mature dams relative to immature dams at mean birth mass. The baseline hazard rate for birth mass was 2.65 and 3.15 kg for neonates born to mature dams and immature dams, respectively (Fig. 4).

For the 8- to 28-d period, no model received more support than the null model (Table 3). Three models were competitive with the null model (birth mass, precipitation, and birth mass + precipitation) for the 8- to 28-d period, but all variables within the competitive models had 95% confidence intervals overlapping 1.

**Discussion**

Contrary to our hypothesis, the absence of predation mortality in our study area did not appear to result in increased neonate survival rate estimates relative to regions with high rates of predation.
Table 2. Summary of AICc values generated by Cox proportional hazard 0- to 7-d survival models for neonates captured at birth sites using vaginal implant transmitters in Sussex County, Delaware, USA (2016 and 2017).

| Model                                      | K  | AICc† | ΔAICc | ΔAICc* |
|--------------------------------------------|----|-------|-------|--------|
| Birth mass + Precipitation 2               | 109.93 | 0.00 | 0.27  |
| Birth mass + Dam maturity                  | 110.13 | 0.20 | 0.25  |
| Birth mass                                 | 110.19 | 0.27 | 0.24  |
| Birth mass + Minimum temp                  | 112.00 | 2.07 | 0.10  |
| Birth mass × Precipitation                 | 113.01 | 3.08 | 0.06  |
| Birth mass × Dam maturity                  | 113.17 | 3.24 | 0.05  |
| Birth mass × Minimum temp                  | 114.35 | 4.42 | 0.03  |
| Global                                     | 117.70 | 7.77 | 0.01  |
| Precipitation 1                            | 120.99 | 11.06 | 0.00  |
| Dam maturity 1                             | 122.33 | 12.41 | 0.00  |
| Null                                       | 122.70 | 12.78 | 0.00  |
| Precipitation + Minimum temp 2             | 122.85 | 12.92 | 0.00  |
| Minimum temp 1                             | 124.22 | 14.29 | 0.00  |
| Precipitation × Minimum temp 1             | 125.85 | 15.92 | 0.00  |
| Birth mass × Precipitation × Minimum temp 1| 126.60 | 16.68 | 0.00  |

† Akaike’s information criterion adjusted for small sample size.
‡ Akaike weight.

Predation mortality. The 90-d survival estimates for neonates captured using VITs (0.44) was comparable to survival estimates from other regions where predation is the primary source of mortality, including 0.49 (Kunkel and Mech 1994) and 0.47 (Carstensen et al. 2009) in Minnesota, 0.47 in Pennsylvania (Vreeeland et al. 2004), 0.42 and 0.44 in two study regions in Missouri (Wright et al. 2019), and 0.45 in the northern forest region of Wisconsin (Warbington et al. 2017). Survival rate to 6 months was 0.36 in a multi-predator system in the Upper Peninsula of Michigan; however, survival rate was not associated with the number of predator species (Kautz et al. 2019). Lesser survival rates are often reported in the southeastern United States and are attributed primarily to predation by coyotes (Kilgo et al. 2012, Chitwood et al. 2015b, Shuman et al. 2017). Kilgo et al. (2010, 2012) posited coyote predation as an additive source of mortality on a study site in South Carolina; however, 3 yr of intensive coyote removal did not result in substantially increased neonate survival (Kilgo et al. 2014). Predator removal efforts also resulted in variable responses in rates of neonate recruitments between two study sites in Georgia (Gulsby et al. 2015). Furthermore, the establishment of coyote populations throughout the eastern and southern United States does not appear to have resulted in changes in deer population dynamics on a large spatial scale (Bragina et al. 2019). In regions with established predator communities, natural mortality not related to predation occurs at a relatively constant proportion across landscape types and generally accounts for <50% of all observed neonate mortalities (Gingery et al. 2018). Natural causes accounted for all the identified mortality in our study, primarily emaciation and disease. Although additive and compensatory mortality sources are difficult to discern, our results suggest non-predation-related mortality sources can produce survival rates similar to neonate population under predation, and the concept of predation as a compensatory mortality source for neonate white-tailed deer may warrant further research.

Necropsy and histological analyses identified several different diseases as primary causes of mortality, including bacterial sepsis, pneumonia, encephalitis, hepatic necrosis, and Theileria cervi parasitism. Lone star ticks (Amblyomma americanum) are the definitive vector for Theileria cervi, which commonly infects healthy individuals but can lead to death at high levels of infestation or in nutritionally stressed individuals (Yabsley et al. 2005, Haus et al. 2018). These diagnoses often require histological analyses, which researchers seldom conduct in neonatal survival studies, and are likely frequently misattributed during field necropsies. Theileria cervi is particularly difficult to identify even with histological examination, meaning disease prevalence was likely greater than our findings suggest (Haus et al. 2018). Emaciation often occurred secondarily to a disease diagnosis, and without histological analyses, we would have likely misattributed these mortality events to starvation. Furthermore, physiologically stressed neonates may vocalize more readily than healthy fawns (Chitwood et al. 2014). In the presence of predators, vocalization provides an auditory cue that could increase the probability of a diseased or emaciated neonate being depredated (Haff and Magrath 2011). Several of the neonates in our study that died from disease or emaciation would have likely been depredated, had predators been present in the region. These
compensatory predation events, while technically not misclassified, would have likely inflated the apparent influence of predation in our system and masked the importance of disease and emaciation in our study area (Chitwood et al. 2014).

Emaciation was the most common contributing factor to mortality for neonates in the study area. Emaciation is typically reported as a minor cause of mortality and is often attributed to maternal abandonment (Ricca et al. 2002, Rohm et al. 2007, Saalfeld and Ditchkoff 2007). We found milk in the stomach and formed fecal pellets in the colon for most of the mortality cases (62%) in which emaciation was listed as the primary cause of death, similar to observations made by Warbington et al. (2017). Additionally, hourly GPS location data from the dams showed frequent visits to the neonate’s location both pre- and postmortem. Given the difficulty of diagnosing diseases and the often-collateral occurrence of emaciation and disease infection, we suspect emaciation in these neonates was a result of undetected pathogens. The risk of maternal abandonment due to capture and handling procedures is low (Carstensen Powell et al., 2005), and we believe abandonment is a convenient but potentially over-reported explanation for emaciation/starvation in neonates.

The disparity in survival rates between capture methods was likely due to a high probability of inobservance of neonate mortality occurring in the first 7 d following parturition. Several studies have reported disproportionately high rates of mortality in the first week of life (Rohm et al. 2007, Carstensen et al. 2009, Kilgo et al. 2012, Shuman et al. 2017). The mean age of opportunistic captures (6 d) was comparable to other research using similar capture methods (Grovenburg et al. 2012, McCoy et al. 2013). Opportunistically captured neonates added to survival analyses via staggered entry have already

Fig. 4. The influence of birth mass on the risk of mortality (log hazard) in the first 7 d of life for neonates captured in Sussex County, Delaware, USA (2016 and 2017), using vaginal implant transmitters. Neonates from mature dams (≥ 4 yr of age) are represented by the dashed orange line, and neonates from immature dams (< 4 yr of age) are represented by the solid gray line. The dashed red line corresponds to the baseline hazard rate, the value at which birth mass had no effect on mortality risk (log hazard = 0).
Table 3. Summary of AICc values generated by Cox proportional hazard 8- to 28-d survival models for neonates captured at birth sites using vaginal implant transmitters in Sussex County, Delaware, USA (2016 and 2017).

| Model                                      | K | AICc† | ΔAICc | AICw‡ |
|--------------------------------------------|---|-------|-------|-------|
| Null                                       | 0 | 84.86 | 0.00  | 0.27  |
| Birth mass                                 | 1 | 85.30 | 0.44  | 0.21  |
| Precipitation                              | 1 | 86.09 | 1.23  | 0.14  |
| Birth mass + Precipitation                 | 2 | 86.76 | 1.90  | 0.10  |
| Dam maturity                               | 1 | 87.14 | 2.28  | 0.08  |
| Minimum temp                               | 1 | 87.15 | 2.29  | 0.08  |
| Birth mass + Minimum temp                  | 2 | 87.91 | 3.05  | 0.06  |
| Birth mass + Dam maturity                  | 2 | 87.92 | 3.06  | 0.06  |
| Precipitation + Minimum temp               | 2 | 88.73 | 3.87  | 0.04  |
| Birth mass × Precipitation                 | 1 | 89.29 | 4.43  | 0.03  |
| Birth mass × Minimum temp                  | 1 | 90.52 | 5.66  | 0.02  |
| Birth mass × Dam maturity                  | 1 | 90.99 | 6.13  | 0.01  |
| Precipitation × Minimum temp               | 1 | 91.79 | 6.93  | 0.01  |
| Global                                     | 4 | 97.76 | 12.90 | 0.00  |
| Birth mass × Dam maturity × Minimum temp   | 1 | 108.40| 23.54 | 0.00  |

† Akaike’s information criterion adjusted for small sample size.
‡ Akaike weight.

survived beyond the period of greatest mortality risk, resulting in artificially inflated estimates of survival (Fieberg and DelGiudice 2009, Yang and Aldrich 2012). Chitwood et al. (2017) modeled the potential impact of capture method on neonatal survival rates and hypothesized the inclusion of opportunistically captured neonates may inflate survival estimates. Our findings agree and empirically demonstrate inflation of left truncated survival estimates until 28 d of life when incorporating opportunistic captures into analyses via staggered-entry designs. A similar inflation of survival estimates was reported in Sitka black-tailed deer neonates (O. hemionus sitkensis), where the inclusion of opportunistically captured neonates with VIT-captured neonates resulted in a 7–23% increase in estimated daily survival to 30 d (Gilbert et al. 2014). Alternatively, the implantation or presence of VITs may have resulted in some physiological disadvantage to neonates (e.g., reduced birth mass), or a disturbance during the hours following parturition may weaken the dam–neonate bond (Cook et al. 1971). However, Swanson et al. (2008) found the use of VITs and subsequent capture procedures did not negatively influence neonate survival. Additionally, the mean birth mass we observed in neonates captured at birth sites (2.9 kg) was comparable to mean birth masses reported in captive populations that did not utilize VITs to locate neonates (Zwank et al. 1992, Schultz and Johnson 1995, Michel et al. 2015).

Both physiological and climatic variables influenced mortality risk during the 0- to 7-d period. Birth mass is well established in the literature as a positive correlate to survival probability (Mech and McRoberts 1990, Saalfeld and Ditchkoff 2007, McCoy et al. 2013, Shuman et al. 2017). Neonates with greater body mass at birth are more likely to overcome early adverse conditions (e.g., disease, weather events, and nutritional deficiencies) relative to smaller individuals. Conversely, relatively fewer studies have failed to detect a relationship between neonate birth mass and survival (Rohm et al. 2007, Grovenburg et al. 2011, Kautz et al. 2019), but these studies included opportunistic captures and used mass at capture, estimated age at capture, and an estimated mass gain rate (e.g., 0.2 kg/d; Carstensen et al. 2009) to calculate birth mass. Even under the assumption that birth mass was estimated accurately, these opportunistically captured neonates have already survived several days. If birth mass is influential to early survival, the inclusion of older individuals would limit the available sample population to neonates with greater mean birth mass and confound the influence of birth mass on survival.

Previous studies have suggested neonate birth mass may increase with dam age (Verme 1989), although maternal body mass is more influential than age (Michel et al. 2015, 2019). We documented increased survival probability in neonates born to mature dams; however, the relationship was not driven by increased birth mass, as we did not find evidence to support a difference in birth mass between neonates born to immature or mature dams. The amount and quality of food resources within a female’s home range are likely a function of both age and dominance status (Appleby 1980, Porter et al. 1991), and nutritional condition of the dam is positively associated with neonate survival probability (Duquette et al. 2014). Sams et al. (1996) observed high rates of neonate starvation attributable to density-dependent malnutrition in dams during lactation, and lactation is more energetically
costly than gestation (Hewitt 2011). Immature females in our study area do not appear to be limited nutritionally during gestation and fetal development but may not be able to meet the nutritional demands of lactation due to their low social dominance and reduced access to quality habitat relative to older females. Such social dominance-related nutritional limitations would account for both the high rate of emaciation we observed in mortalities and the greater risk of mortality for neonates born to immature dams. Additionally, age can serve as a proxy for maternal experience, and older dams may be more successful at raising offspring independent of birth mass (Ozoga and Verme 1986, Michel et al. 2015).

Daily precipitation was positively associated with neonate mortality risk in the first 7 d of life. The presence of precipitation was reported to increase daily risk of mortality by a factor of 3 in a highly agricultural site in Wisconsin but had little influence on survival in a more forested site (Warbington et al. 2017). Similar contrasting effects occurred in Texas, where precipitation increased mortality risk in east Texas and decreased risk in the more arid west Texas (Ginnett and Young 2000). The influence of precipitation appears to be scale-dependent, with monthly precipitation totals being positively associated with neonate survival in the Great Plains region (Michel et al. 2018). Increased precipitation totals over longer temporal periods increase the quantity and quality of plant forage available to lactating dams, which likely improves neonate survival (Therrien et al. 2008, Michel et al. 2018). Conversely, increased precipitation totals over a relatively shorter temporal period impact a neonate’s ability to effectively thermoregulate (Grovenburg et al. 2010, Warbington et al. 2017, Michel et al. 2018).

Increased thermoregulatory requirements lead to increased expenditures of energy which can draw-down on already limited resources of smaller or malnourished individuals (Putman et al. 1996, Mysterud and Ostbye 1999), particularly in the first days of life. The influence of daily precipitation on survival is likely complicated regionally by maternal condition and experience, available thermal cover, temperature, and neonate body size. While we did not find evidence to support an interaction effect of birth mass and precipitation on daily mortality risk, greater energy reserves associated with increased birth mass can likely help offset thermoregulatory demands.

No variable influenced neonate survival after the 0- to 7-d period, likely because as neonates age and transition out of the hiding behavior stage, the influence of maternal behavior on survival is reduced (Schwede et al. 1994, Costelloe and Rubenstein 2015). Our results suggest that by 8–28 d postpartum, neonates with low birth mass have either died or have largely overcome early nutritional deficiencies. As neonates become more mobile, dams can access areas of higher quality food resources (Van Moorter et al. 2009), which likely improves the quantity and quality of nutrition the neonate receives through nursing. Similarly, as neonates increase in age, size, and nutritional condition, the importance of thermoregulation to survival is reduced (Van Moorter et al. 2009). While risk of mortality is greatest in the first days of life, risk from predation can increase as neonates become more mobile and begin following the dam (Nelson and Woolf 1987, Lingle et al. 2005, Costelloe and Rubenstein 2015). While we did not detect an influence of any variable on neonate survival beyond 7 d in the absence of predators, maternal experience and birth mass may continue to be influential in regions with predators. Furthermore, predation events occurring after the first week of life may transition to an additive source of mortality as neonates age. While speculative, such a temporal shift between compensatory and additive mortality may explain the lesser rates of neonate survival observed in the southeastern United States (Kilgo et al. 2012, Chitwood et al. 2015b, Shuman et al. 2017), where predation risk persists past the first weeks of life.

**Conclusions**

Without a clear understanding of the compensatory vs. additive mortality dynamic, management efforts attempting to increase neonate survival by means of limiting mortality due to predation may be misguided. Our findings show that natural mortality not related to predation is likely the ultimate mechanism influencing neonatal survival rates in our study area. In regions with abundant predator communities,
depredation may serve as a more proximal and easily identifiable mortality cause but may be primarily compensatory. In these areas, management strategies aimed at increasing neonate survival via predator removal are likely to be ineffective, potentially explaining the results observed by Kilgo et al. (2014) and Gulsby et al. (2015). Additionally, our results are the first to empirically demonstrate that opportunistic capture methods inflated estimates of neonate survival and potentially masked the importance of emaciation and disease-related mortality. Future research should avoid the use of opportunistic capture methods when study objectives include analysis of early-life survival and cause-specific mortality.

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