Landscape-Level Patterns in Fawn Survival Across North America

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ABSTRACT A landscape-level meta-analysis approach to examining early survival of ungulates may elucidate patterns in survival not evident from individual studies. Despite numerous efforts, the relationship between fawn survival and habitat characteristics remains unclear and there has been no attempt to examine trends in survival across landscape types with adequate replication. In 2015–2016, we radiomarked 98 white-tailed deer (*Odocoileus virginianus*) fawns in 2 study areas in Pennsylvania. By using a meta-analysis approach, we compared fawn survival estimates from across North America using published data from 29 populations in 16 states to identify patterns in survival and cause-specific mortality related to landscape characteristics, predator communities, and deer population density. We modeled fawn survival relative to percentage of agricultural land cover and deer density. Estimated average survival to 3–6 months of age was 0.414 ± 0.062 (SE) in contiguous forest landscapes (no agriculture) and for every 10% increase in land area in agriculture, fawn survival increased 0.049 ± 0.014. We classified cause-specific mortality as human-caused, natural (excluding predation), and predation according to agriculturally dominated, forested, and mixed (i.e., both agricultural and forest cover) landscapes. Predation was the greatest source of mortality in all landscapes. Landscapes with mixed forest and agricultural cover had greater proportions and rates of human-caused mortalities, and lower proportions and rates of mortality due to predators, when compared to forested landscapes. Proportion and rate of natural deaths did not differ among landscapes. We failed to detect any relationship between fawn survival and deer density. The results highlight the need to consider multiple spatial scales when accounting for factors that influence fawn survival. Furthermore, variation in mortality sources and rates among landscapes indicate the potential for altered landscape mosaics to influence fawn survival rates. Wildlife managers can use the meta-analysis to identify factors that will facilitate comparisons of results among studies and advance a better understanding of patterns in fawn survival. © 2018 The Wildlife Society.

KEY WORDS fawn, meta-analysis, North America, *Odocoileus virginianus*, survival, white-tailed deer.

Landscape structure and composition affect wildlife population dynamics by modifying the source and frequency of mortality (Hahn and Hatfield 1995, Donovan and Jones 1997, Ellis et al. 2012). The relative frequency of mortality in different landscapes can provide insight into factors that influence population persistence (Collins and Kays 2011). Survival rates of neonates of large herbivore species vary across North American landscapes and neonate survival is an important source of variation in population growth rates. Neonatal survival is sensitive to changes in population density and habitat characteristics when compared to older life stages (Pettorelli et al. 2003). As such, identifying landscape-level patterns in neonate survival may provide a better understanding of factors that influence population growth.

Given that white-tailed deer (*Odocoileus virginianus*) occupy a diversity of landscapes across North America, accounting for variation in fawn survival requires understanding how landscapes influence mortality. Agriculture has assisted in recovery of generalist predator species (Oehler and Litvaitis 1996), altered spatial concentration of quality deer food sources (Sol et al. 2013), and increased human-related disturbances that lead to fawn mortality (e.g., agricultural activities such as hay mowing, roads). Agricultural landscapes generally occur on more productive soils than forested landscapes, which may increase availability of high-quality forage from crops that can complement natural food sources

for pregnant or nursing females (Mautz 1978, Shaw et al. 2010, Hewitt 2011). As a result, females in agricultural landscapes with access to higher quality food resources may experience an elevated individual nutritional state and rear fawns that experience greater growth rates (Therrien et al. 2008). Sources of potential optimal foraging opportunities in agricultural landscapes, however, could be contrasted by human-related disturbances (e.g., hay mowing, vehicles) and lead to increased fawn mortality. Furthermore, human-dominated landscapes may alter predator-prey interactions (Rodewald et al. 2011).

Another factor potentially influencing fawn survival is population density. Among K-selected (i.e., density-dependent and slow-paced life histories) and iteroparous species, high population density can adversely affect body condition and reduce recruitment and survival via increased intraspecific competition (Clutton-Brock et al. 1987, Simard et al. 2014). Intraspecific competition limits forage availability and results in density-related responses via social stress, disease transmission, or behavioral modification (Ozoga and Verme 1986, Putman et al. 1996). For example, Ozoga et al. (1982) suggested competition for space in high-density populations could lead to lack of isolation in mother-fawn pairs and subsequent improper bonding and higher fawn mortality. However, it can be difficult to detect how population size alone may influence various population dynamics because the level of intraspecific competition is partially determined by the population size relative to critical limiting resources (Bowyer et al. 2014). Ultimately, early life stages are likely the first to experience negative effects of increased population density (e.g., reduced body size at birth and slower growth rates) for long-lived vertebrate species and the consequences of these negative effects may not be offset later in life (Eberhardt 1977, Hewison et al. 2002).

A meta-analysis of fawn survival studies could elucidate patterns in fawn survival not evident within a single region or population. Individual studies often limit the ability to detect patterns in survival because site-specific differences influence fawn mortality (Pettorelli et al. 2005, Shuman et al. 2017). Despite decades of research, uncertainty about the relationship between fawn survival and habitat remains. Individual studies accounting for how microhabitat characteristics (e.g., vegetation height) and macrohabitat characteristics (e.g., forest patch density) influence fawn survival are often contradictory and do not adequately represent the association between fawn survival and habitat characteristics at larger spatial scales. Previous studies suggest certain microhabitat characteristics at bed sites may increase white-tailed deer fawn survival (Brinkman et al. 2004, Grovenburg et al. 2010); however, Chitwood et al. (2015) reported only weak support for this conclusion. A positive association between macrohabitat characteristics within a fawn's home range, and fawn survival observed by (Rohm et al. 2007) was not observed by similar studies (Vreeland et al. 2004, Grovenburg et al. 2011). Furthermore, although mortality rates vary greatly among landscapes, hypotheses that address the cause of this variation are conflicting. For example, heterogeneous landscapes can support greater densities of predators (Oehler

and Litvaitis 1996) even though prey in heterogeneous landscapes can experience lower mortality rates as predators exploit alternative (human-created) food resources (Stephens et al. 2005, Rodewald et al. 2011). Recent studies regarding potential landscape-scale characteristics that affect fawn survival lack replication among representative landscapes and limit the ability to differentiate between the effects of landscape-scale habitat characteristics and regional differences (Rohm et al. 2007, Gulsby et al. 2017).

We conducted a meta-analysis of white-tailed deer fawn survival, combined with our own data, to evaluate how demographic and environmental variables influence survival and mortality. First, we hypothesized fawn survival is related to landscape-level land use, and predicted that fawn survival would be higher in agricultural landscapes that provide high-quality foraging opportunities. Second, we investigated the source and rate of cause-specific mortality among landscapes. We predicted 1) a greater proportion and rate of human-caused deaths in agricultural landscapes, 2) a lower proportion and rate of predation-caused deaths in mixed landscapes (i.e., both forest and agricultural land cover) because adult females and fawns exploit security cover in forested patches and forage in nearby agricultural patches, and 3) a lower proportion and rate of natural-caused fawn deaths (excluding predation) in agricultural landscapes because agricultural landscapes generally occur on more productive soils, which would suggest that females have access to higher quality forage (natural and cultivated) and may produce fawns in better condition. Also, we investigated the relative amount of mortality attributed to canids, black bear (*Ursus americanus*), and bobcat (*Lynx rufus*) and predicted 4) a lower proportion and rate of canid predation in mixed landscapes when compared to forested and agricultural landscapes because of the availability of alternative food sources for predators. Finally, we hypothesized that fawn survival is related to deer density and predicted lower fawn survival in high-density deer populations because of increased intraspecific competition.

STUDY AREA

We monitored fawn survival and cause-specific mortality in 2 study areas in Pennsylvania (Fig. 1). The northern study area (NS; 155 km^2) was located in the Susquehannock State Forest in Potter County and part of the Deep Valleys section of the Appalachian Plateaus physiographic region (Cuff et al. 1989). Pennsylvania lies within the humid continental climate zone and the seasons were characterized by cold winters (mean temperature = 24.2°F) and humid summers (mean temperature = 68.8°F) with the majority of precipitation occurring in spring and early summer (Northeastern Regional Climate Center [NRCC] 2018). The NS topographic features were plateaus at approximately 800-m elevation dissected by steep drainages at approximately 220 m. In the region surrounding the NS, the Northwest Plateau, the mean annual temperature was 47.4°F and mean annual precipitation was 45.61 inches (NRCC 2018). A mixture of northern hardwoods and conifer forest types comprised 88% of the NS based on the 2015 National
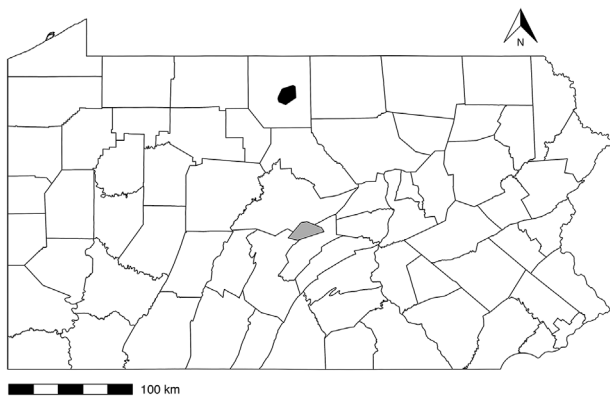
Figure 1. A northern study area (NS; black) and a southern study area (SS; gray) of white-tailed deer fawn survival and cause-specific mortality in Pennsylvania, USA, 2015–2016.

Agricultural Statistics Service Cropland Data Layer. Dominant tree species were red maple (*Acer rubrum*), sugar maple (*Acer saccharrum*), black cherry (*Prunus serotina*), and American beech (*Fagus grandifolia*). Agricultural land cover (row crops, hay and alfalfa fields, pastures) comprised <1% of the total NS land area. Remaining land cover was open water, roads, and others. Pre-hunting season deer densities in the NS were 9.2 deer/km².

The southern study area (SS; 239 km²) was in Centre, Mifflin, and Huntingdon counties in the Ridge and Valley physiographic region in central Pennsylvania (Cuff et al. 1989). The SS contained 178 km² of Rothrock State Forest and approximately 6 km² of Bald Eagle State Forest. Topographic features consisted of long, parallel ridges and valleys along a northeast-southwest axis (Cuff et al. 1989). In the Central Mountain Region of Pennsylvania that surrounded the SS the mean annual temperature was 48.0°F and mean annual precipitation was 44.82 inches (NRCC 2018). Agricultural land cover (row crops, hay, alfalfa, and pastures) comprised 15% of the total SS land area. The oak-hickory forest type usually contained an understory layer of ericaceous shrub species (*Vaccinium* spp., *Gaylussacia* spp., *Gaultheria procumbens*, and *Kalmia latifolia*) and comprised 79% of the land area. Dominant tree species were red and white oaks (*Quercus* spp.) along with red maple, black birch (*Betula lenta*), black gum (*Nyssa sylvatica*), and hickory (*Carya* spp.). Pre-hunting season deer densities in the SS were approximately 10.3 deer/km². Potential fawn predator species in both study areas included black bear, coyote (*Canis latrans*), red fox (*Vulpes vulpes*), grey fox (*Urocyon cinereoargenteus*), and bobcat (*Lynx rufus*). Harvest and population data indicated predator densities were higher in NS than in SS (Rosenberry 2009, Johnson 2016).

METHODS

To assist in fawn captures, we captured adult female deer from January to April 2015–2016 using rocket nets and single-gate clover traps (Hawkins et al. 1968, Carstensen et al. 2009), and inserted a vaginal implant transmitter (VIT; Vectronic Aerospace, Berlin, Germany) under protocols

approved by The Pennsylvania State University Institutional Animal Care and Use Committee (Protocol No. 47054). To insert a VIT, we sedated female deer with a 150-mg intramuscular injection (IM) of xylazine hydrochloride and following the procedure, reversed sedation with 150 mg of tolazoline hydrochloride given by intramuscular injection. Also, we administered a 1,400-mg intramuscular injection of oxytetracycline if cuts and abrasions occurred during capture.

We fitted females with a global positioning system (GPS) satellite radio-collar (GPS Plus, Vectronic Aerospace, Berlin, Germany) linked to the VIT, so that when the VIT was expelled, the change in temperature of the VIT signaled the GPS collar to transmit a message that a potential birth had occurred. We waited ≥6 hours after receiving notification of expulsion before initiating searches to ensure a social bond was established between mother-fawn pairs (Kilgo et al. 2012). We conducted additional searches 8–48 hours after the initial search if we did not locate fawns.

During 10 May to 15 June in 2015 and 16 May to 7 July in 2016, we used a fawn bleat (Diem 1954, Vreeland et al. 2004) to provoke postpartum maternal behaviors in free-ranging adult females (White et al. 1972, Ozoga et al. 1982) during vehicle searches along roads and trails (Vreeland et al. 2004, Rohm et al. 2007, Grovenburg et al. 2012). If we observed maternal behavior or an isolated female, a team of 2–5 people conducted a grid search of the immediate area. Crews in the SS also searched hay and clover fields, with or without sightings of a female, on private lands.

We marked fawns with a numbered, plastic tag in each ear (National Band and Tag, Newport, KY, USA) imprinted with a toll-free telephone number and notification of a $100 reward if found and reported. We fitted each fawn with an expandable, very high frequency (VHF) radio-collar (Vectronic Aerospace or Advanced Telemetry Systems, Isanti, MN, USA). Fawn collar transmitters remaining motionless for 4 hours transmitted a signal indicating a possible mortality.

We monitored survival of radio-collared fawns via ground-based telemetry twice daily from capture until mid-August, 1–7 times weekly from mid-August through early December, and 1–3 times weekly thereafter until mortality or collar failure. We investigated all fawn mortality within 24 hours of signal detection. We noted vegetative disturbance, carcass condition, presence of predator scat or prints, and any predator-specific kill characteristics to identify the likely predator species (Vreeland et al. 2004). We identified causes of mortality via information obtained from the mortality site and carcasses. We collected carcasses for necropsy at the Pennsylvania State University Animal Diagnostic Laboratory. We classified cause of death as predation, human-caused, natural (excluding predation), and unknown.

We used known-fate models in Program MARK version 6.1 (White and Burnham 1999) to estimate weekly fawn survival. We estimated survival at 26 weeks of age because this is common in other studies (Huegel et al. 1985, Nelson and Woolf 1987, Decker 1992, Kunkel and Mech 1994). We constructed 3 candidate models for the NS and SS to investigate the influence of using VITs to capture fawns on

estimates of fawn survival and decided *a priori* to incorporate a time variable into every model (i.e., survival varied by week). The 3 models of fawn survival included 1) only a time effect (S[week]), 2) lower survival for fawns captured using VITs (an additive model where the difference between groups was constant on the logit scale; S[week + VIT]), and 3) survival for fawns captured using VITs differed from fawns captured opportunistically (S[week × VIT]). We compared models using Akaike's Information Criterion adjusted for sample size (AIC$_c$; Burnham and Anderson 2002). We selected the model with the lowest AIC$_c$ as the best model. We considered fawns at risk from date of capture and estimated survival by weeks since capture to meet the assumption that all individuals had the same mortality risk in each time period (Pollock et al. 1989). We censored fawns when we recovered a transmitter with no evidence of mortality.

Meta-Analysis

We used Google scholar and EBSCO host to search for published reports (both peer-reviewed and theses) of white-tailed deer fawn survival in North America and included studies that reported fawn survival rate, sample size, and cause-specific mortality. Most mortality in many ungulate species occurs during the first 8 weeks of life (Linnell et al. 1995) so we considered 3–6-month survival rates comparable. As a result, all studies used in the meta-analysis provided survival estimates for 3–6 months after birth. When evaluating how fawn mortality varied among landscapes, we excluded studies that did not detail land cover type (i.e., forest, agriculture).

To investigate the association between fawn survival and landscape-level land use, we performed a weighted linear regression using the package stats in Program R (R Development Core Team 2016), in which the weights were study sample size. We included studies that provided fawn survival rate, sample sizes, and reported landscape cover (e.g., forest, agriculture) as percentages. We used fawn survival rate as the response variable and percentage of agricultural land cover as the independent variable. Forested land cover and agricultural land cover were inversely related ($r = -0.963$, $n = 14$); therefore, we did not include percent forest cover as an independent variable. We compared the land cover model to an intercept-only model using AIC$_c$ (Burnham and Anderson 2002). If multiple years were reported, we averaged survival rates. Also, we averaged the land cover percentages for studies by Rohm et al. (2007) and Grovenburg et al. (2011, 2012), which reported land cover statistics for 2 study areas but a single fawn survival rate. We tested assumptions of normality of the residuals and equal variances using a Shapiro-Wilks test and a plot of residuals versus predicted values, and used $\alpha = 0.05$ to infer statistical significance.

We classified cause of death into 3 categories: human-caused (e.g., harvest, illegal harvest, roadkill, fence entanglement), natural excluding predation (e.g., malnutrition, disease, abandonment, drowning), and predation. We calculated the proportion (i.e., the source) and rate (proportion × mortality rate) of mortality causes. We calculated proportions from all recorded instances of death for studies that reported cause-specific mortality information and described the dominant land cover type in their study area. We determined how human-caused, natural, and predation-caused mortality rates varied among landscapes using studies that presented cause-specific mortality, survival estimate for 3–6 months of age, and land cover descriptions. We calculated the proportion and rate of canid predation (i.e., coyote and domestic dog predation) because it is difficult to distinguish between coyote and domestic dog predation when assigning cause of death.

We calculated mortality rates by multiplying the proportion of death attributed to a certain source by the reported mortality rate (1–survival rate) for each study. Because we used proportional mortality data, we used a logit transformation, $\log_e(p/[1-p])$, to satisfy the assumptions of linear modeling (Warton and Hui 2011) for all proportions throughout analyses. We replaced zero values in the mortality proportion data with the minimum non-zero value (Warton and Hui 2011).

We identified 3 landscape categories (i.e., agriculture, forest, mixed landscapes) and classified land cover as majority forest or agriculture when these land types comprised of >70% of the land area. Agricultural landscapes were composed of cultivated land, pasture, and grassland. We classified landscapes with <70% forest or <70% agriculture that contained both agricultural and forested cover as mixed. For example, we classified Burroughs et al. (2006) as a mixed landscape because it contained 54% agricultural and 32% forest (i.e., neither forest nor agriculture composed >70% of the landscape). We used data from studies that expressed landscape composition in explicit percentages and studies that stated whether agriculture or forest were dominant vegetative types in their study area.

We used analysis of variance (ANOVA) to test for differences between 1) the proportion and rate of predation-, human-, and natural-caused deaths, 2) the proportion and rate of predation-caused deaths among forested, mixed, and agricultural landscapes, 3) the proportion and rate of human-caused deaths among landscapes, 4) the proportion and rate of natural-caused deaths among landscapes, 5) the proportion of black bear, bobcat, and canid predation, and 6) proportion and rate of canid predation among landscapes. If the normality assumption was violated, we performed a non-parametric Kruskal–Wallis test for differences among proportion and rates.

We used a weighted linear regression to test the association between fawn survival and deer population density (deer/km^2) and deer density/forested km^2 using the package stats in Program R (R Development Core Team 2016). We used fawn survival rate as the response variable and deer density (or deer density/forested km^2) as the independent variable weighted by sample size. We tested assumptions using the Shapiro-Wilks test for normality and a plot of residual versus fitted values. We compared this model to an intercept-only model using AIC$_c$. We used the midpoint of density

estimates if a range of deer densities was reported. For example, Kilgo et al. (2012) reported a deer density of 4–$8\,deer/km^2$ and we used a deer density of $6\,deer/km^2$.

RESULTS

Field Study

We captured 98 fawns: 43 fawns in the SS and 55 in the NS. Of the 98 radio-collared fawns, 36 died and 15 were censored by 26 weeks. We captured 16 fawns using VITs: 4 fawns in the SS and 12 in the NS. Survival at 26 weeks was 0.51 (95% CI = 0.37–0.65) in the NS and 0.71 (95% CI = 0.55–0.83) in the SS. Analysis of survival to 26 weeks indicated fawn survival varied by week in the SS (AIC_c weight = 0.598) and the NS (AIC_c weight = 0.657; Table 1). Sample sizes were too small to estimate parameters for both models that included an effect for method of capture (S[week + VIT] and S[week × VIT]).

Proportions of mortality by cause were similar between the NS and SS ($X_3^2 = 5.7$, $P = 0.055$). Predation was the leading cause of death in the NS, but in the SS predation and natural deaths were the leading sources of mortality. The source of predation differed between the NS and SS ($X_3^2 = 9.0$, $P = 0.028$); black bears accounted for most predation deaths in the NS and bobcat predation was most prevalent in the SS.

Meta-Analysis

Twenty-six publications of 29 populations met the criteria for inclusion in the meta-analyses of the 37 publications we found across the range of white-tailed deer in North America (Fig. 2; see Table S1, available online in Supporting Information). The current field study, Vreeland et al. (2004), and Warbington et al. (2017) described their 2 study areas in enough detail to treat each study area as a separate population.

We found a positive relationship between the amount of agricultural land cover and fawn survival ($R^2 = 0.502$, $P = 0.004$; Table 2; Fig. 3), which was better than an intercept-only model ($\Delta AIC_c = 5.87$). The linear model was:

$$\hat{S} = 0.414 + 0.0049 \times (\%agriculture),$$

where fawn survival to 3–6 months of age averaged 0.414 ± 0.062 (SE) in contiguous forest landscapes (no agriculture) and for every 10% increase in land area in agriculture, fawn survival increased 0.049 ± 0.014. The 3
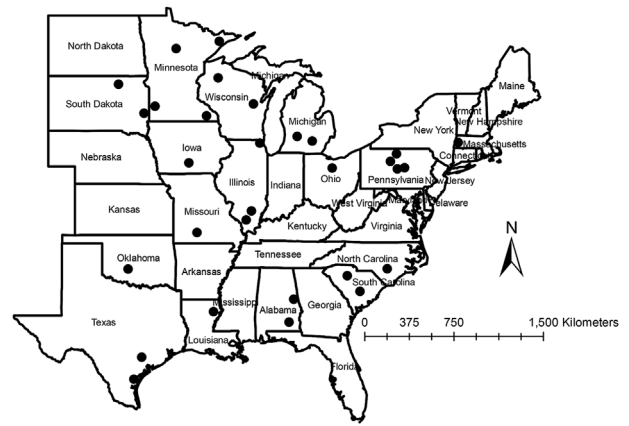

Figure 2. Locations of 29 white-tailed deer populations included in 26 studies of 3–6-month-old fawn survival and cause-specific mortality across North America used in a meta-analysis of fawn survival, 1965–2016.

lowest survival rates occurred in the southeastern United States (Kilgo et al. 2012, Chitwood et al. 2015, Shuman et al. 2017), but even if we excluded these data, the relationship remained significant ($R^2 = 0.435$, $P = 0.027$), and survival increased 0.029 ± 0.011 (SE) for every 10% increase in agricultural land cover.

The proportion of deaths attributed to predation-, human-, and natural-causes differed ($X_3^2 = 50.080$, $P < 0.001$; Fig. 4A) as did the rate of mortality due to predation-, human-, and natural-causes ($X_3^2 = 23.223$, $P < 0.001$; Fig. 4B). Predation was the largest source of death; proportions of predation ($\bar{x} = 0.657$, 95% CI = 0.558–0.745) were greater than proportions of human-caused ($\bar{x} = 0.069$, 95% CI = 0.047–0.101) and natural deaths ($\bar{x} = 0.185$, 95% CI = 0.131–0.255). Natural deaths were a greater source of mortality than human-caused deaths. However, the rate fawns died from natural causes ($\bar{x} = 0.068$, 95% CI = 0.042–0.107) was similar to the rate fawns died from human-causes ($\bar{x} = 0.031$, 95% CI = 0.019–0.050). Predation rate ($\bar{x} = 0.236$, 95% CI = 0.158–0.338) was greater than human-caused mortality rate and natural-caused mortality rate. The assumption of normality was not met for these analyses, so we used Kruskal–Wallis tests. All other analyses hereafter met the assumption of normality and we used ANOVA with the logit transform of proportions and rates.

Table 1. Model selection statistics for 3 models describing white-tailed deer fawn survival (S) in the northern study area (NS) and southern study area (SS) within 26 weeks of capture, central Pennsylvania, USA, 2015–2016.

	NS				SS			
Model	ΔAIC_c[a]	w_i[b]	−2 log-likelihood	K[c]	ΔAIC_c[a]	w_i[b]	−2 log-likelihood	K[c]
S(week)	0.0	0.66	148.8	26	0.0	0.60	96.5	26
S(week + VIT[d])	1.3	0.34	147.9	27	0.8	0.40	95.1	27
S(week × VIT)	52.0	0.00	142.5	52	52.7	0.00	91.5	52

[a] Difference in corrected Akaike's Information Criterion (AIC_c) value from the model with the lowest AIC_c value.
[b] AIC_c weight.
[c] Number of parameters.
[d] Vaginal implant transmitter.

Table 2. White-tailed deer fawn (3–6 months old) survival, population density (deer/km²), land cover statistics, and land cover category for studies of fawn survival in North America, 1992–2016, including the current study in the northern study area (NS) and southern study area (SS) in central Pennsylvania.

State	Study	Sample size	Survival rate	Density (deer/km²)	Forest (%)	Agriculture (%)	Landscape
MI	Burroughs et al. (2006)	75	0.90[a]	19	32	54	Mixed
MA	Decker (1992)	37	0.75[b]	7	71	14	Forest
SD	Grovenburg et al. (2012)	81	0.75[c]	3	2.3	83.4	Agriculture
SD and MI	Grovenburg et al. (2011)	78	0.87[c]		2.65	91.55	Agriculture
MI	Hiller et al. (2008)	32	0.62[b]	27	13.4	52.3	Mixed
IL	Rohm et al. (2007)	166	0.59[d]		45	45.5	Mixed
PA	Vreeland et al. (2004)	110	0.58[b]	8	38	40	Mixed
PA	Vreeland et al. (2004)	108	0.45[b]		87	0	Forest
PA	Current study (NS)	55	0.51[b]		88	0.75	Forest
PA	Current study (SS)	43	0.71[b]		79	15	Forest
SC	Kilgo et al. (2012)	91	0.23[e]	6	90	0	Forest
LA	Shuman et al. (2017)	70	0.27[f]	19.5	88.7	8.5	Forest
NC	Chitwood et al. (2015)	65	0.14[e]	3	71	0	Forest
MI	Carstensen et al. (2009)	66	0.47[f]	11			
AL	Jackson and Ditchkoff (2013)	14	0.26[b]	11			
MN	Kunkel and Mech (1994)	21	0.49[g]	3.5			
OH	Kennedy (2015)	57	0.78[b]	12.6			
WI	Warbington et al. (2017)	89	0.65[h]	9.5	80	0	Forest
WI	Warbington et al. (2017)	139	0.45[h]	25			

[a] Survival to 127 days.
[b] Survival to 180 days.
[c] Survival 15 May–31 August.
[d] Survival to 21 May–1 October.
[e] Survival to 16 weeks.
[f] Survival to 12 weeks.
[g] Survival May–October.
[h] Survival to 110 days.

The source (i.e., the proportion) and rate (proportion × mortality rate) of cause-specific mortality differed among landscapes (Table 4). Although predation was the leading source of death in all landscapes, proportions of predation and predation rate differed among landscapes (Tables 3 and 4). In mixed landscapes, we detected lesser proportions of predation and predation rates compared to forested landscapes. Also, we predicted a greater proportion of human-caused deaths in agricultural landscapes; however,
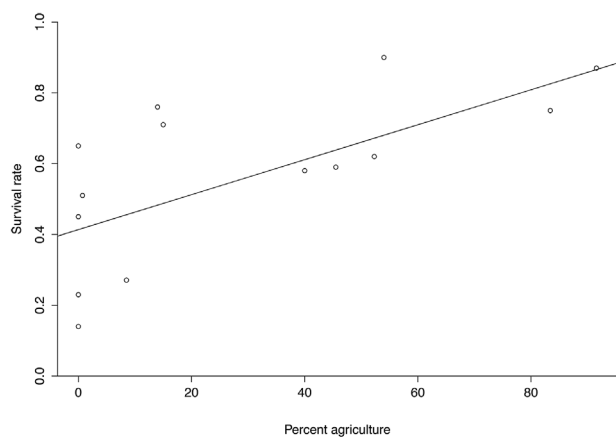

Figure 3. Positive relationship (weighted by sample size) between survival rate of 3–6-month-old white-tailed deer fawns and percentage of agriculture within the study area, North America, 1992–2016. Fawn survival to 3–6 months of age averaged 0.414 ± 0.062 (SE) in contiguous forest landscapes (no agriculture) and for every 10% increase in agricultural land cover, fawn survival increased 0.049 ± 0.014.

proportions of human-caused deaths and human-caused mortality rates were greater in mixed landscapes when compared to forested landscapes (Table 4). Although we predicted natural-caused deaths would be a smaller source of mortality in agricultural landscapes, we did not detect any differences among the proportion or rate of natural-caused mortality among landscapes (Table 4). Furthermore, although predation was lesser in mixed landscapes when predator species were considered together, we did not detect any differences in the proportion of canid-related deaths or canid predation rate among landscapes (Table 4).

Canid, bobcat, and black bear predation were not similar sources of mortality ($F_{2, 52} = 20.58$, $P < 0.001$). The proportion of canid predation ($\bar{x} = 0.401$, 95% CI = 0.297–0.515) was greater than the proportion of bobcat predation ($\bar{x} = 0.067$, 95% CI = 0.041–0.109; $P < 0.001$) and bear predation ($\bar{x} = 0.165$, 95% CI = 0.083–0.302; $P = 0.025$). Proportions of bobcat and bear predation were similar ($P = 0.092$). Too few studies with black bear or bobcat present were available to investigate differences in predation rates among species.

We predicted fawn survival would be lower in high deer density populations. However, we failed to detect a relationship between deer density (deer/km², $P = 0.782$; Fig. 5A) or deer/forested km² ($P = 0.099$; Fig. 5B) and fawn survival (Table 2).

DISCUSSION

By conducting a meta-analysis of fawn survival rates, we detected patterns in fawn survival at a landscape-level that
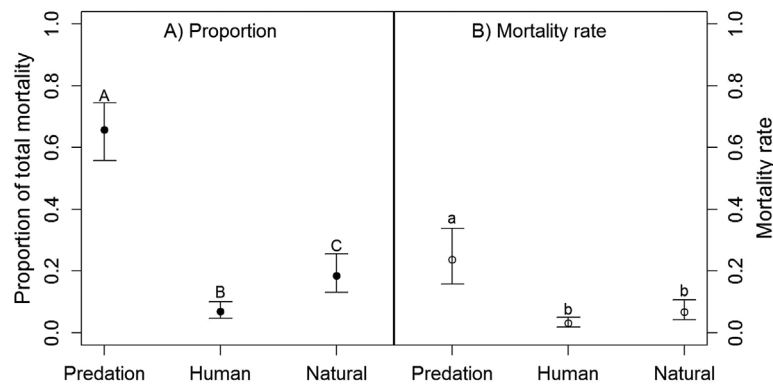
Figure 4. Means and 95% confidence intervals for Kruskal-Wallis tests of the proportion (A) and mortality rate (B) of predation, human-caused, and natural deaths for 3–6-month-old white-tailed deer fawns. We used the data in a meta-analysis of fawn mortality across North America, 1971–2016. Proportions do not sum to 1.0 because we did not graph unknown mortality causes. Proportions that are statistically different from each other are denoted by different uppercase letters ($\alpha = 0.05$). Mortality rates statistically different from each other are denoted by different lower case letters ($\alpha = 0.05$).

were not evident from individual studies. Associations between habitat characteristics and fawn survival remain unclear within individual studies. A limited spatial perspective may explain conflicting results because examination of life-history characteristics in large herbivores is sensitive to the scale of observation (Hewitt 2011). To our knowledge, this meta-analysis is the first examination of the association

between habitat characteristics and fawn survival with replication among landscape types.

Multiple studies conducted within the 3 landscape categories strengthen inferences that the differences in fawn survival detected by the meta-analysis were due to landscape-scale habitat characteristics rather than region-specific differences; however, there are several potential

Table 3. Number of mortalities by cause and predator for 3–6-month-old white-tailed deer fawns and land cover category for 26 populations in North America, 1965–2016.

State	Reference	Number of mortalities	Cause-specific mortality			Predators			Landscape
			Human	Natural	Predation	Black bear	Bobcat	Canid[a]	
OK	Bartush and Lewis (1981)	43	0	3	38	NP[b]	2	23	
MI	Burroughs et al. (2006)	7	3	3	1	NP	NP	1	Mixed
MN	Carstensen et al. (2009)	28	0	0	24	9	9	NP	Forest
TX	Carroll and Brown (1977)	47	0	10	28	NP	0	28	Mixed
NC	Chitwood et al. (2015)	55	1	16	35	NP	5	30	Forest
TX	Cook et al. (1971)	58	0	10	48	NP	2	46	
MA	Decker (1992)	7	1	1	5	NP	1	3	Forest
SD	Grovenburg et al. (2012)	23	6	5	12	NP	NP	10	Agriculture
SD & MI	Grovenburg et al. (2011)	15	0	3	12	NP	NP	12	Agriculture
MI	Hiller et al. (2008)	10	4	1	4	NP	NP	4	Mixed
IA	Huegel et al. (1985)	13	1	2	10	NP	NP	10	Agriculture
AL	Jackson and Ditchkoff (2013)	9	0	2	7	NP	1	6	Forest
SC	Kilgo et al. (2012)	70	0	8	57	NP	6	43	Forest
MI	Kunkel and Mech (1994)	9	0	0	9	4	NP	NP	Forest
SC	McCoy et al. (2013)	68	2	15	29	NP	7	14	Forest
IL	Nelson and Woolf (1987)	24	6	0	13	NP	NP	13	Mixed
IL	Piccolo et al. (2010)	27	2	0	25	NP	NP	25	Forest
IL	Rohm et al. (2007)	64	3	5	41	NP	3	26	Mixed
AL	Saalfeld and Ditchkoff (2007)	24	0	7	15	NP	NP	10	
MN	Schulz et al. (1983)	7	0	4	NP	NP	NP	NP	Mixed
LA	Shuman et al. (2017)	51	0	5	45	17	11	9	Forest
PA	Vreeland et al. (2004)	43	17	18	8	1	0	5	Mixed
PA	Vreeland et al. (2004)	55	5	11	39	15	3	13	Forest
MO	Dalton (1985)	38	2	17	18	NP	4	8	
PA	Current study (NS[c])	25	1	3	21	11	0	6	Forest
PA	Current study (SS[d])	11	1	5	5	1	2	1	Forest
OH	Kennedy (2015)	22	13	5	3	NP	NP	3	
WI	Warbington et al. (2017)	42	0	2	35	9	8	5	Forest
WI	Warbington et al. (2017)	43	4	21	15	1	1	10	Agriculture

[a] Canid includes coyotes and domestic dogs because it is difficult to distinguish between coyote and domestic dog predation when assigning cause of death.
[b] NP = species was not present.
[c] Northern study area.
[d] Southern study area.

Table 4. Means and 95% confidence intervals for 8 analyses of variance (each represented by a separate row) for 3–6-month-old white-tailed deer fawn mortality sources (proportion of mortality) and mortality rate among forested, mixed (i.e., both forest and agriculture cover), and agricultural landscapes in North America, 1965–2016. Mortality rates are defined as the proportion of mortality for each cause of death × mortality rate. Proportions do not add to 1.0 because we excluded the proportion of unknown mortality causes from the table.

Analysis type Cause-specific mortality	Landscape type			F	P
	Forested	**Mixed**	**Agriculture**		
Proportions					
Predation	0.782 (0.678–0.860)[a]	0.396 (0.229–0.591)[b]	0.626 (0.388–0.815)[a,b]	$F_{2, 20} = 6.932$	0.005
Natural deaths	0.141 (0.090–0.215)[a]	0.229 (0.129–0.372)[a]	0.249 (0.117–0.453)[a]	$F_{2, 20} = 1.545$	0.237
Human-caused deaths	0.029 (0.016–0.052)[a]	0.257 (0.133–0.436)[b]	0.111 (0.041–0.268)[a,b]	$F_{2, 20} = 13.310$	<0.001
Canid predation[c]	0.368 (0.205–0.568)[a]	0.337 (0.144–0.606)[a]	0.570 (0.256–0.837)[a]	$F_{2, 18} = 0.631$	0.543
Rates					
Predation	0.412 (0.281–0.556)[a]	0.086 (0.034–0.198)[b]	0.139 (0.050–0.329)[a,b]	$F_{2, 15} = 8.562$	0.003
Natural deaths	0.072 (0.041–0.124)[a]	0.056 (0.021–0.138)[a]	0.077 (0.025–0.208)[a]	$F_{2, 15} = 0.151$	0.862
Human-caused deaths	0.014 (0.007–0.026)[a]	0.069 (0.024–0.186)[b]	0.033 (0.009–0.110)[a,b]	$F_{2, 15} = 3.950$	0.042
Canid predation[c]	0.159 (0.074–0.309)[a]	0.067 (0.019–0.206)[a]	0.113 (0.028–0.362)[a]	$F_{2, 15} = 1.561$	0.242

[a,b] Numbers with the same letter are not different from each other, whereas numbers with different letters are different within a row ($\alpha = 0.05$).

[c] Canid includes coyotes and domestic dogs because it is difficult to distinguish between coyote and domestic dog predation when assigning cause of death.

weaknesses in a meta-analysis approach. We assumed similar spatial structure within forested landscapes because quantifying the level of landscape heterogeneity, patch sizes, or vegetation structure and composition among landscapes was not possible. Similarly, the agricultural landscape category included grassland and pasture, but we could not evaluate differences within agricultural landscapes such as agriculture cover type (e.g., soybeans, corn), which might influence nutrient availability. Evaluating fawn survival in agricultural landscapes and differentiating among crop types (i.e., corn, soybean, cotton) could provide more insight regarding the relationship between agriculture and fawn survival. Using a meta-analysis approach to evaluate landscape-level effects of land cover type is challenging, but large herbivores make decisions at large scales and can move among landscapes (Hebblewhite and Merrill 2009). Thus, it is important to understand how land cover affects large herbivore dynamics at a landscape level.

Sampling unit differences across studies (i.e., study area size) and different methodologies can produce variation in survival and density estimates and cause-of-death determination. For example, relying on fawn searches may result in an overestimation of fawn survival if you are less likely to capture fawns that die within a few days of birth (Gilbert et al. 2014, Chitwood et al. 2017). The use of VITs has recently become widespread in fawn survival studies. As a result, we combined studies that used opportunistic capture methods (i.e., grid searches) and more recent studies that use VITs in the meta-analysis. However, when we excluded studies that used VITs, we still found the same relationship between survival and percentage of agriculture on the landscape ($n = 8$, $R^2 = 0.582$, $P = 0.046$).

Overall fawn survival was positively associated with agricultural land cover, which supports hypotheses of a higher nutritional plane potential in agricultural landscapes benefiting lactating females (Hewitt 2011, Warbington et al. 2017). White-tailed deer population declines have been described in landscapes where agricultural land cover exceeds 75%, but we did not observe lesser fawn survival in Grovenburg et al. (2011, 2012) where the study area's agricultural land cover exceeded 75% in comparison to other studies in the meta-analysis where agricultural land cover did not exceed this threshold (Hewitt 2011). However, in contradiction to the hypothesis of agricultural landscapes providing higher quality deer forage and offsetting starvation and disease-related deaths, we did not find less fawn mortality due to natural causes in agricultural landscapes. Natural sources of mortality (e.g., starvation, abandonment) occurred in similar proportions across all landscape types. These findings suggest that agricultural land cover increases fawn survival but probably not by reducing the rate of natural-caused mortality.
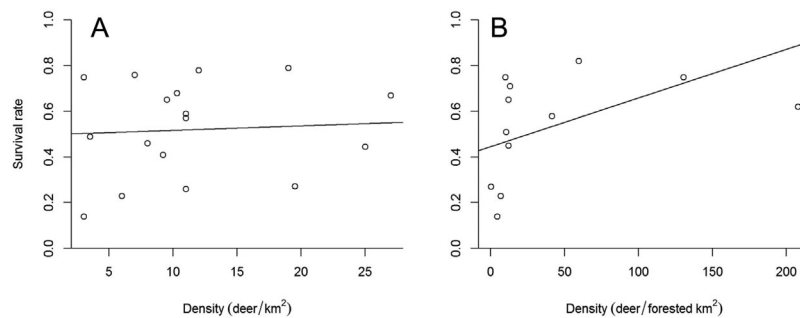

Figure 5. Linear regressions (weighted by sample size) of the association between 3 and 6-month-old white-tailed deer fawn survival rate to deer density (A), $y = 0.496 + 0.002\times$, with y representing fawn survival rate and x representing deer density (deer/km^2) and deer per forested km^2 (B), $y = 0.445 + 0.002\times$, with y representing fawn survival rate and x representing deer per forested km^2 in North America, 1992–2016.

Although speculative, it is plausible the result of similar rates of natural-causes mortality among landscapes might be confounded because we defined natural-caused mortality as any deaths deemed abandonment, disease, and starvation. Starvation-related deaths could be affected by nutrients within a landscape, whereas abandonment and disease may not, resulting in similar natural-caused deaths among landscape types. Also, factors other than nutrient availability could have influenced the greater fawn survival we observed in agriculture areas. Unfortunately, the meta-analysis could not address questions of the mechanisms for the observed mortality patterns.

Compared to natural-caused deaths and predation, Linnell et al. (1995) indicated that human activity (e.g., killed by agricultural machinery and vehicle collisions) plays a relatively small role in ungulate neonate mortalities; however, our results partially contradict this finding. Although humans were the smallest source of mortality, natural and human-caused deaths occurred at similar rates, suggesting human stressors may play a greater role than previously thought. Human-causes were the smallest source of mortality, but mixed landscapes had greater rates and proportions of human-caused deaths when compared to forested landscapes. In mixed landscapes, the combination of mowing-related deaths, hunter harvest, and vehicle collisions resulted in greater human-caused mortality than in forested landscapes.

Predation was the most common cause of death, but proportions of predation differed among landscapes, indicating land-use changes by humans may alter predator-prey dynamics. Fawns are a temporally limited food resource and lack specialized predators; consequently, their generalist predators may make trade-offs between human-created food resources (e.g., crops) and fawns (Burroughs et al. 2006, Mattisson et al. 2016). As such, human activity can create a low-risk–high-forage scenario for prey in landscapes with greater human influence (Rodewald et al. 2011). Alternatively, opportunistic omnivores such as black bears may encounter fawns while seeking reliable human-created food resources and increase fawn predation risk in landscapes with greater human influence (Bastille-Rousseau et al. 2011). Nevertheless, the proportion and rate of predation-related deaths were less in mixed landscapes when compared to forested landscapes, suggesting human activities or effects may reduce predation risk.

Similar predation rates between forested and agricultural landscapes suggest human activity alone does not explain lower predation rates in mixed landscapes. Mixed landscapes are more heterogeneous and contain more edge when compared to forested landscapes. It remains unclear how edge habitat affects predation, but at the landscape-level we observed less predation in heterogeneous landscapes. Contrary to observations of reduced coyote predation risk for fawns with increased edge habitat within their home range (Rohm et al. 2007, Gulsby et al. 2017), we did not observe a lesser proportion of canid predation in mixed landscapes even though overall predation rates were lower. More research is needed at multiple spatial scales to determine how mixed landscapes influence predation rates

and predator densities. For example, high-contrast edges are commonly associated with greater predator densities (Oehler and Litvaitis 1996), potentially increasing fawn predation risk in these areas. Alternatively, edges may harbor fewer predators (Cherry et al. 2017), provide alternative food resources for predators, and increase predator foraging efficiency among cover types, resulting in lower predation rates (Burroughs et al. 2006, Rohm et al. 2007, Gulsby et al. 2017).

Canid predation was a greater source of mortality than black bear or bobcat predation. Coyotes are commonly listed as the primary predator within studies and are a source of additive mortality in the southeastern United States (Kilgo et al. 2012, Watine and Giuliano 2015). Black bears accounted for similar, or greater, proportions of mortality when compared to coyotes in several studies we reviewed (Ballard et al. 1999, Vreeland et al. 2004). However, because we could not determine the rate of black bear predation, inferences concerning how these sources of predation influenced fawn survival is limited. Estimating coyote and black bear predation rates would provide insight into the relative influence of these predators on fawn survival and may be particularly important for multi-predator systems (Shuman et al. 2017).

We may have failed to detect a relationship between fawn survival and deer/km^2 or deer/forested km^2 because density alone does not reflect the population size relative to carrying capacity, which would determine the level of intraspecific competition within a landscape (Bowyer et al. 2014). We investigated both measures of density because other behaviors (e.g., dispersal) depend on deer density per unit of forest on the landscape (Long et al. 2005, Lutz et al. 2015). Environmental quality influences a system's carrying capacity and the effect of density-dependent factors, such as forage availability (Iijima and Ueno 2016). Disentangling the effects of co-occurring density-dependent and density-independent factors is difficult (Pierce et al. 2012). For instance, Bowyer et al. (2014) noted that although winter severity is commonly listed as density independent, the resource availability afforded to populations well below carrying capacity could result in greater survival because of a physiological buffer against such weather. Consequently, covariation in carrying capacity and deer density likely contributed to a lack of detection of a relationship between fawn survival and population density.

Developing a better understanding of ungulate life-history characteristics necessitates examination of population dynamics at multiple spatial scales and with a level of uniformity among studies to allow comparison. We could not include results from several studies in the meta-analysis because of ambiguity in their reporting of cause-of-death and survival rates (e.g., survival reported at 26 weeks, but cause-of-death summarized at 1 year), and poorly detailed study area descriptions. Even so, we detected patterns at a landscape level not evident from individual studies. Patterns detected by the meta-analysis underscore the importance of considering landscape characteristics when examining survival at early life stages. Future studies may consider land

cover type and arrangement at several spatial scales within their region because these factors can influence survival and mortality risk (Gulsby et al. 2017).

MANAGEMENT IMPLICATIONS

For managers and decision-makers concerned with fawn recruitment, the results of the meta-analysis indicate efforts to alter fawn survival will be challenging. Although predation was the largest source of mortality and occurred at the greatest rates, predator control efforts are difficult and often unsuccessful. Managers looking to influence fawn mortality by increasing structural diversity and maintaining a heterogeneous landscape structure with a mix of agriculture and forest may observe less fawn predation. However, greater rates of human-caused mortalities in mixed landscapes may offset fewer predation-related deaths. Thus, alternative management approaches, such as reduced antlerless harvests, may be more effective at achieving deer population objectives than attempts to manipulate the factors that influence fawn mortality. Ultimately, recruitment rates, for a given reproductive rate, likely will be lower in forested landscapes. In populations above desired densities, antlerless harvest may have to be proportionally greater in agriculturally dominated landscapes than forested landscapes given the greater fawn survival. The broad patterns in fawn survival highlighted by the meta-analysis, however, are best considered in conjunction with local monitoring efforts because fawn survival is influenced by site-specific differences (Shuman et al. 2017).

ACKNOWLEDGMENTS

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