Survival rates, mortality causes, and habitats of Pennsylvania white-tailed deer fawns

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Abstract Estimates of survival and cause-specific mortality of white-tailed deer (*Odocoileus virginianus*) fawns are important to population management. We quantified cause-specific mortality, survival rates, and habitat characteristics related to fawn survival in a forested landscape and an agricultural landscape in central Pennsylvania. We captured and radiocollared neonatal (<3 weeks) fawns in 2000–2001 and monitored fawns from capture until death, transmitter failure or collar release, or the end of the study. We estimated survivorship functions and assessed influence on fawn survival of road density, habitat edge density, habitat patch diversity, and proportion of herbaceous habitat. We captured 110 fawns in the agricultural landscape and 108 fawns in the forested landscape. At 9 weeks after capture, fawn survival was 72.4% (95% CI=63.3–80.0%) in the agricultural landscape and 57.2% (95% CI=47.5–66.3%) in the forested landscape. Thirty-four-week survival was 52.9% (95% CI=42.7–62.8%) in the agricultural landscape and 37.9% (95% CI=27.7–49.3%) in the forested landscape. We detected no relationship between fawn survival and road density, percent herbaceous cover, habitat edge density, or habitat patch diversity (all $P>0.05$). Predation accounted for 46.2% (95% CI=37.6–56.7%) of 106 mortalities through 34 weeks. We attributed 32.7% (95% CI=21.9–48.6%) and 36.7% (95% CI=25.5–52.9%) of 49 predation events to black bears (*Ursus americanus*) and coyotes (*Canis latrans*), respectively. Natural causes, excluding predation, accounted for 27.4% (95% CI=20.1–37.3) of mortalities. Fawn survival in Pennsylvania was comparable to reported survival in forested and agricultural regions in northern portions of the white-tailed deer range. We have no evidence to suggest that the fawn survival rates we observed were preventing population growth. Because white-tailed deer are habitat generalists, home-range-scale habitat characteristics may be unrelated to fawn survival; therefore, future studies should consider landscape-related characteristics on fawn survival.

Key words black bear, *Canis latrans*, coyote, fawn, habitat, hunting, landscape, mortality, *Odocoileus virginianus*, Pennsylvania, predation, survival, *Ursus americanus*, white-tailed deer

Knowledge of survival and mortality rates of fawns is important for managing white-tailed deer (*Odocoileus virginianus*) populations (White and Lubow 2002). Several studies have assessed neonatal mortality of white-tailed deer in North America (e.g., Huegel et al. 1985, Nelson and Woolf 1987, Decker et al. 1992, Long et al. 1998, Ballard et al. 1999). However, relative to the extensive range of white-tailed deer, the distribution of fawn mortality studies is limited. Fawn mortality studies elsewhere

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have identified predation, legal and illegal harvest, disease, starvation, malnutrition, parasites, accidents, collisions with vehicles and farm machinery, and other causes of mortality. However, no consistent regional or landscape-related mortality patterns are discernible.

Estimates of annual fawn mortality attributed to coyote (*Canis latrans*) predation range from 0 to near 100% (Porath 1980, Linnell et al. 1995). Many factors contribute to this variability, but no studies have asserted that coyote predation suppresses white-tailed deer populations for extended periods. Black bears (*Ursus americanus*), red foxes (*Vulpes vulpes*), gray foxes (*Urocyon cinereoargenteus*), and bobcats (*Lynx rufus*) also prey on fawns, but their effect has not been quantified.

Understanding the influence of hunting mortality is crucial to setting appropriate harvest limits. However, most information on fawn hunting mortality comes from harvest data. Fawn-to-doe kill ratios, age structure of a harvest, and proportion of fawns in the harvest can be biased estimates of the true proportion of fawns killed by legal hunting because not all age and sex classes of deer have the same probability of harvest or probability of being reported as harvested (Roseberry and Woolf 1991, 1998; Xie et al. 1999). Also, hunters may be less likely to report small or antlerless deer (Steinert et al. 1994). A direct estimate of hunting mortality can be obtained from radiomarked deer.

Vegetation association, extent, and arrangement can influence predator and prey communities, and therefore might influence fawn survival. Predator behavior and hunter access and efficacy also can be influenced by other habitat features, including road type and density, and habitat composition and configuration. Landscape-scale habitat relations have been defined for white-tailed deer in some regions (Roseberry and Woolf 1998). However, influence of home-range-scale habitat characteristics on white-tailed deer fawn survival has not been investigated.

For 2 areas with different topographic, vegetative, and physical features, our objectives were to 1) quantify cause-specific mortality of white-tailed deer fawns, 2) estimate survival rates of fawns, and 3) quantify influence of habitat characteristics within fawn home ranges on fawn survival.

Study areas

Penns Valley (PV) in Centre County was an agricultural valley located approximately 30 km east of State College in Pennsylvania's Ridge-and-Valley physiographic province. Most valley land was devoted to agriculture; common crops were corn, soybeans, hay, alfalfa, and grains. Annual and perennial herbaceous land cover (row crops, hay and alfalfa fields, pastures) was 40% of total PV land area. Small hardwood woodlots were located on agriculturally unproductive areas, around farmsteads and housing developments, and along riparian corridors. Slopes and ridges surrounding PV were typical eastern oak (*Quercus* spp.)–hickory (*Carya* spp.)–red maple (*Acer rubrum*) forest, and deciduous forests and woodlots comprised 38% of total PV land cover. Development was limited to low-density rural housing and small hamlets and villages. Deer hunting occurred throughout PV, but much private land was posted.

Comprising approximately 200 km^2, the Quehanna Wild Area (QWA) was located in Moshannon and Elk state forests in Elk, Cameron, and Clearfield counties in the Appalachian Plateau physiographic province. Two paved roads bisected QWA, and numerous dirt roads, hiking and snowmobile trails, and natural gas and electric utility corridors were located throughout the area. Forest cover primarily was second- and third-growth mature hardwoods (75% of total QWA land area) and regenerating stands (12%) with few, small, and scattered herbaceous openings (6%), including utility corridors. A distinct browse line created by deer was evident throughout much of QWA. Elk (*Cervus elaphus*) also contributed to the browse line, but elk density during our study in QWA was $\leq$0.3 elk/km^2 (C. Rosenberry, Pennsylvania Game Commission [PGC], personal communication). The QWA was public land with no restrictions on number of hunters pursuing antlered deer, but the number of antlerless licenses was restricted.

Both study areas supported a diversity of potential fawn predators including black bears, coyotes, foxes, and bobcats. Harvest and population data for black bears, bobcats, and coyotes suggested that predator densities were greater in QWA than in PV (Lovallo 1999; PGC, unpublished data). Detailed descriptions of study areas are available in Vreeland (2002).

Methods

Fawn searches

We captured fawns from 16 May–25 June in 2000 and from 22 May–21 June in 2001. The capture period coincided with the statewide median date of fawn births estimated from fetal data collected from pregnant, vehicle-killed does (PGC, unpublished data).

We located bedded fawns via foot searches during 2000 and 2001 in PV and during 16 May–1 June in 2000 in QWA. Foot-search crews consisted of 6–10 persons. In PV, crews concentrated search effort in old fields and active hay and alfalfa fields, woodlots, and generally <200 m into contiguous forest. We traversed search areas in segments so that entire areas were completely searched.

In QWA we searched for fawns and observed female behavior via vehicle searches along roads, trails, and utility corridors. We used a fawn bleat call (Diem 1954, Arthur et al. 1978) to elicit maternal behavior (Downing and McGinness 1969, White et al. 1972, Lund 1975, Ozoga et al. 1982, Heister 1995). When we observed requisite behavior from does, we conducted brief, localized foot searches for fawns.

Capture and handling

We captured fawns by hand, sometimes with the aid of salmon landing nets (0.9-m hoop diameter, 1.2-m handles). We blindfolded fawns to minimize stress during processing. We used 7.5-kg or 11-kg scales and canvas sacks or cotton pillowcases to weigh fawns. We minimized scent transferal among fawns and between handlers and fawns by limiting handling time and the number of persons handling each fawn, requiring handlers to wear latex gloves, processing fawns >10 m from the site of capture, partially stuffing sacks with grasses and leaf litter (changed after each fawn), and frequently washing weighing sacks without soap. We took care to keep fawns upright during processing to prevent injury to internal organs.

Each fawn received a uniquely numbered, brown plastic tag in each ear (Original™ tags, Temple Tag Co., Temple, Tex.). Each tag was imprinted with a toll-free telephone number to enable persons recovering tagged fawns to notify the PGC. We fitted each fawn with a brown, expandable, 97-g VHF radiocollar (Advanced Telemetry Systems, Inc., Isanti, Minn.; Diefenbach et al. 2003). Transmitters were equipped with an inactivity sensor, which doubled the pulse rate if motionless for 4 hours. Transmitters deployed in 2001 were equipped with a mortality coding that recorded the number of 0.5-hour intervals the collar had remained motionless after the initial 4-hour motionless period.

Survival monitoring and mortality assessment

We used ground-based telemetry to monitor fawn survival 1–3 times daily from capture through mid-August, 1–7 times weekly from mid-August through early December, and 1–3 times weekly thereafter. We monitored all fawns until death, transmitter failure or collar release, or the study's end (12 months in 2000–2001, 9 months in 2001–2002).

When we received a transmitter signal in inactive mode, we located the collar and attempted to determine the fate of the fawn. When predation was suspected, we identified predators and distinguished predation from scavenging by assessing carcass condition, predator sign, vegetation condition at the site, and by comparing evidence to published descriptions of predator-specific kill and scavenging characteristics (Cook et al. 1971, Beale and Smith 1973, White 1973, O'Gara 1978, Ozoga and Verme 1982). When evidence could not conclusively identify one predator, but predation was known as cause of death, we classified the cause as "unidentified predator." When we were unable to determine cause of death in the field, veterinarians at the Pennsylvania State University Animal Diagnostic Laboratory (PSUADL) conducted a necropsy and tested for presence of disease and parasites. We classified mortalities into these categories: predation, natural causes excluding predation, vehicle collisions, farm-machinery collisions, poaching, hunting harvest, crop-depredation harvest, accidents, unidentified mortalities, and censors.

Location and home-range estimation

Using ground-based telemetry, we located fawns via triangulation ≥1 time weekly. In 2000 we plotted telemetry bearings on United States Geological Survey 1:24,000 topographic maps to assess bearing precision in the field. In 2001 we used LOAS v. 2.04.2 (Location Of A Signal, Ecological Software Solutions, Sacramento, Calif.). We used only those locations with a 95% chi-square error ellipse ≤4.0 ha (79.2% of locations had error ellipses <0.6 ha, White and Garrott 1990). No bias was evident (95% confidence arcs included zero) in bearing angle errors for telemetry observers (Vreeland 2002).

Using KERNELHR (Seamann et al. 1998), we calculated 95% fixed-kernel home ranges for fawns having ≥10 locations at 9 weeks after capture. We then calculated median home-range size by site and year. Few or no locations were available to define home ranges for fawns dying within one week of collaring. Therefore, we created a circular buffer area within which to assess habitat composition and configuration. Buffers were the same area as year- and site-specific median home ranges (40.1 ha for PV fawns and 61.5 ha for QWA fawns in 2000, and 48.2 ha for PV fawns and 69.7 ha for QWA fawns in 2001 [Vreeland 2002]).

GIS and habitat analyses

We used a Geographic Information System (GIS) to assess land cover and characteristics of habitat composition and configuration. We obtained 30-m grid cell resolution of vegetative land cover (water, evergreen forest, mixed forest, deciduous forest, woody transitional [shrubs, regenerating forest], perennial herbaceous, annual herbaceous, barren [hard surface, gravel, rubble, pavement, etc.]), and state and local road data from the Pennsylvania Spatial Data Access website (http://www.pasda.psu.edu). We calculated total road density and area of land-cover types within each fawn's buffer zone. From area estimates we calculated the proportion of annual and perennial herbaceous land cover within fawn buffer areas. For land cover within each buffer zone, we calculated 2 metrics of habitat configuration: edge density (McGarigal and Marks 1995) and patch diversity as measured by Simpson's diversity index (SDI; McGarigal and Marks 1995) using Patch Analyst Grid (Elkie et al. 1999).

Survival analyses

Known fates. We used the known-fates (KF) procedure in program MARK v. 2.1 (White and Burnham 1999, Cooch and White 2002) to model survival and estimate survival rates. We used a 7-day period to record capture, death, and censor events. When we recovered only a transmitter, and no evidence indicated fawn death, we censored the fawn at the time of collar recovery. Because 70.8% of mortalities occurred within 9 weeks of capture (Vreeland 2002), we suspected the shape of survivorship curves during these initial 9 weeks would have the greatest influence on differences in survival between sites and years. Therefore, we estimated survival rates and modeled survival within 9 weeks of capture. Estimates of survival at 6 months (26 weeks or 180 days) are common in other fawn-survival studies (Huegel et al. 1985, Nelson and Woolf 1987, Decker et al. 1992, Kunkel and Mech 1994, Long et al. 1998, Ballard et al. 1999). Therefore, to permit comparisons between studies, we also report survival rates at 26 and 34 weeks after capture.

We captured fawns during 3- to 5-week periods in 2000 and 2001; therefore, to meet assumptions of the staggered-entry survival model (Pollock et al. 1989), we classified all fawns at risk from a common starting time (i.e., entries were not staggered) regardless of the actual date they were radiocollared. Mortality and censor events corresponded to the number of weeks the fawn had been alive, rather than the calendar date of death or censor.

We developed 13 models of fawn survival incorporating grouping variables (study site, year, fawn sex) and individual covariates (mass at capture, days between capture date and statewide median annual fawn drop). We used Akaike's Information Criterion, corrected for small sample size (AIC_c), to select the model that best described fawn survival (Burnham and Anderson 1998) and report survival rates and log-normal 95% confidence intervals (CI) generated by MARK.

Logistic regression. We used logistic regression (PROC LOGISTIC, SAS v. 8.1, Statistical Analysis System, Cary, N.C.) to identify the relation between fawn survival at 9 weeks and habitat characteristics (road density, edge density, SDI, proportion of herbaceous habitat), but also included grouping variables (study site [PV = 1, QWA = 0], year, fawn sex) and individual covariates (mass at capture, days between capture date and median annual fawn drop). We used AIC to select the model that best described fawn survival. We used the Hosmer and Lemeshow goodness-of-fit test to assess fit of the global model in PROC LOGISTIC.

We calculated survival rates and proportions of mortality causes through 34 weeks post-capture because we were interested in documenting survival and mortality from birth through hunting seasons in mid-January. To determine whether causes of mortality were the same between years, we conducted a chi-square homogeneity test, pooling mortality causes when cell counts would have resulted in expected values <5.

Results

We captured 218 fawns: 52 in PV and 46 in QWA in 2000, and 58 in PV and 62 in QWA in 2001. Within 34 weeks of capture, 106 of 218 radiocollared fawns died and 21 were censored (Table 1).

Table 1. Percentage of deaths (n = 106) by cause of mortality within 34 weeks of capture of 218 radiomonitored white-tailed deer fawns in Penns Valley (PV, n = 47) and Quehanna Wild Area (QWA, n = 59), central Pennsylvania, May–January, 2000–2002.

	PV		QWA	
Mortality cause	%	95% CI	%	95% CI
Predation	17.0	9.2–31.5	69.5	58.7–82.3
Natural causes[a]	38.3	26.7–54.9	18.6	11.0–31.4
Vehicles	14.9	7.7–28.9	3.4	1.0–11.6
Hunting	10.6	4.8–23.5	3.4	1.0–11.6
Farm machinery	6.4	2.3–17.8		
Poaching	2.1	0.4–10.7	3.4	1.0–11.6
Bizarre accidents[b]	4.3	1.3–14.6		
Deer depredation[c]	4.3	1.3–14.6		
Unknown[d]	2.1	0.4–10.7	1.7	0.3–8.6
Censored[e]	12.7	7.8–20.6	6.5	3.2–13.0

[a] Excludes predation. Causes were starvation, malnutrition, malnourishment, emaciation, forced weaning, colostrum deprivation, failure to nurse, enteritis, necrotic enteritis, acute enteritis, catharrhal enteritis, gastroenteritis, edema, brain edema, lung edema, necrosis, hepatic necrosis, zenker necrosis, heart muscle degeneration, hemorrhage, brain hemorrhage, adrenal hemorrhage, low liver selenium, vitamin deficiency, bronchopneumonia, pneumonia, dehydration, overheating, exhaustion, infection, naval infection, gangrene, nephrosis, renal nephrosis, clostridium perfringens, coccidiosis, corona virus, diarrhea, emphysema, enteropathy, hemorrhagic enteropathy, focal brain microabscess, giardia, giardiasis, hepatitis, leptospirosis, nephritis, salmonella, and tapeworm infestation. Considerable overlap within and among fawns existed. Individual fawns may have had multiple conditions.

[b] One fawn fell down an abandoned well and another became entangled in a fence.

[c] Legally killed by farmers holding deer depredation permits.

[d] No carcasses were found. Collars were cut off fawns and discarded within 10 m of major roadways. Fawns were struck by vehicles, poached, or legally harvested during a January hunting season.

[e] Contact was lost with transmitter or only collars were recovered with no evidence to suggest death occurred. These percentages not included in column totals.

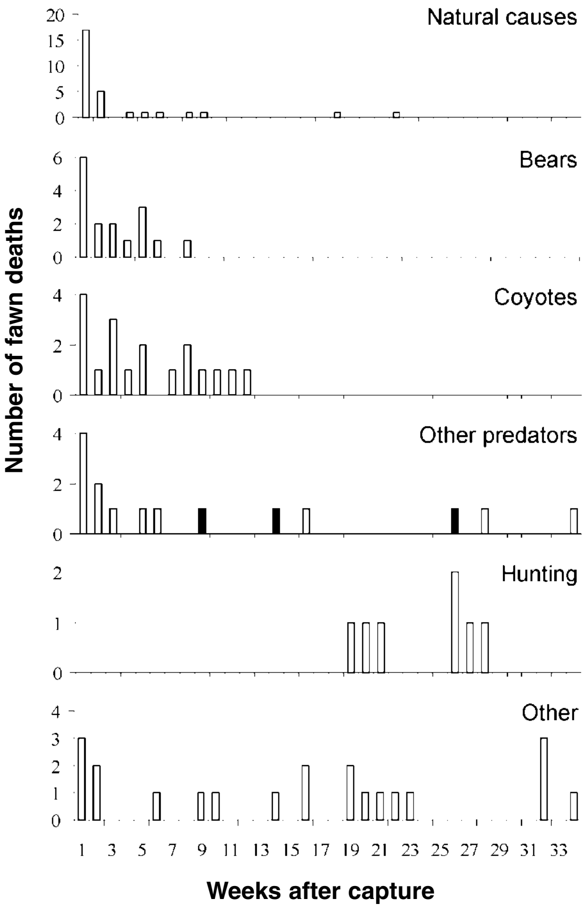

Figure 1. Number of deaths of white-tailed deer fawns within 34 weeks after capture attributed to natural causes (excluding predation), bears, coyotes, unidentified predators (open bars) and bobcats (solid bars), hunting, and all other causes of mortality (collisions with vehicles and farm machinery, poaching, harvest under deer depredation permits, and unknown mortalities), central Pennsylvania, May–January, 2000–2002. Note different scales on *y*-axes.

Fawn mass at capture was not greater in QWA ($\bar{x}$= 4.38 kg, SE=0.11 kg, n=104) than in PV ($\bar{x}$=4.13 kg, SE=0.11 kg, n=97; t_{199}=-1.68, P=0.094).

Mortality causes

Proportions of mortality were similar between 2000 and 2001 (χ^2_2=4.3, P=0.116) (Table 1). Most (70.8%) fawns died within 9 weeks of capture: 83.7% of predation events and 93.1% of deaths attributed to natural causes, excluding predation, occurred within 9 weeks after capture (Figure 1).

Natural causes, excluding predation, were the leading cause of mortality in PV (Table 1). Veterinarians at the PSUADL identified malnutrition or starvation as a factor in 21 of 29 deaths attributed to natural causes through 34 weeks. Thirteen (61.9%) of these 21 instances of starvation-related mortality occurred within 3 days of capture, 3 (14.3%) occurred within 7 days of capture, and 5 (23.8%) fawns died from starvation or malnutrition 10–37 days after capture.

Predation accounted for 69.5% (95% CI = 58.7–82.3%) of mortalities in QWA and 17.0% (95% CI = 9.2–31.5%) of mortalities in PV (Table 1). Proportion of fawns killed by predators differed between PV and QWA, but proportions of fawn deaths attributed to other causes of mortality were similar between PV and QWA (Table 1). In QWA,

Table 2. Percentage of predation mortalities (n = 49) within 34 weeks of capture of white-tailed deer fawns attributed to bears, coyotes, bobcats, and unidentified predators in the Quehanna Wild Area (QWA, n = 41) and Penns Valley (PV, n = 8), central Pennsylvania, May–January, 2000–2002.

	PV		QWA	
Predator species	%	95% CI	%	95% CI
Coyote	62.5	36.9–100.0	31.7	20.4–49.4
Bear	12.5	2.6–59.1	36.6	24.6–54.5
Bobcat			7.3	2.6–20.2
Unidentified	25.0	8.3–75.6	24.4	14.4–41.4

bears and coyotes combined were responsible for statistically similar predation rates (Table 2).

Survival

Known fates. The best model (AIC_c weight = 95.0%) suggested that fawn survival within 9 weeks of capture differed between QWA and PV and over time (Table 3, Figure 2). Models that incorporated effects of year, sex, mass at capture, days departure from median date of fawn drop, or combinations of these covariates were inferior ($\Delta AIC_c \geq 5.95$, Table 3). Survival at 1 week post-capture was 83% in both PV and QWA, but survival subsequently decreased more rapidly in QWA (Figure 2). Survival at 9 weeks after capture was 72.4% (95% CI = 63.3–80.0%) in PV and 57.2% (95% CI = 47.5–66.3%) in QWA. Survival at 26 weeks after capture was 58.6% (95% CI = 48.8–67.7%) in PV and 45.6% (95% CI = 36.0–55.6%) in QWA. Thirty-four week survival was 52.9% (95% CI = 42.7–62.8%) in PV and 37.9% (95% CI=27.7%–49.3%) in QWA.

Logistic regression. The global model fit the data ($\chi^2_8 = 12.449$, $P = 0.132$). In the best model, only study site and fawn mass at capture were related to fawn survival at 9 weeks after capture. The probability of a fawn surviving (Y) was given as

$$\text{logit}(Y) = -1.559 + 0.758\ (\text{study site}) + 0.403\ (\text{fawn mass at capture}),$$

where study site was coded 1 for PV and 0 for QWA. Standard errors for estimates were 0.613 for the intercept, 0.303 for study area, and 0.132 for fawn mass. Habitat characteristics were not related to overall fawn survival at 9 weeks after capture ($\Delta AIC_c > 2$). Fawns in PV were 2.14 (95% CI = 1.18–3.87) times more likely to survive through 9 weeks after capture than fawns in QWA, and survival probability increased by 1.50 (95% CI =

Table 3. Performance of 13 candidate models describing white-tailed deer fawn survival within 9 weeks of capture, central Pennsylvania, 2000–2001.

Model	Model description	k[a]	ΔAIC_c[b]	w[c]
S (site × time)	Survival varies through time and between sites	18	0.00	0.9501
S (time)	Survival varies through time	9	5.95	0.0484
S (year × time)	Survival varies through time and between years	18	13.02	0.0014
S (year × site × time)	Survival varies through time and among years and sites	36	21.21	0.0000
S (mass)	Survival varies by fawn mass at capture	2	51.16	0.0000
S (date, mass)	Survival varies by fawn mass at capture and days between capture date and date of peak fawn drop within year	3	53.01	0.0000
S (site)	Survival varies between sites	2	59.03	0.0000
S (year + site)	Survival at both sites differs between years by a constant value	3	59.96	0.0000
S (year × site)	Survival varies between years and sites	4	61.97	0.0000
S (year)	Survival varies between years	2	64.06	0.0000
S (date)	Survival varies by days between capture date and date of peak fawn drop within year	2	64.70	0.0000
S (site + time)[d]	Survival covaries through time with a constant difference between sites	10		
S (year + time)[d]	Survival covaries through time with a constant difference between years	10		

[a] Number of parameters in model.
[b] Difference between Akaike's Information Criteria, corrected for small sample size, and the model with the lowest AIC_c.
[c] AIC_c relative weight attributed to model.
[d] Models failed because numerical convergence was not achieved.

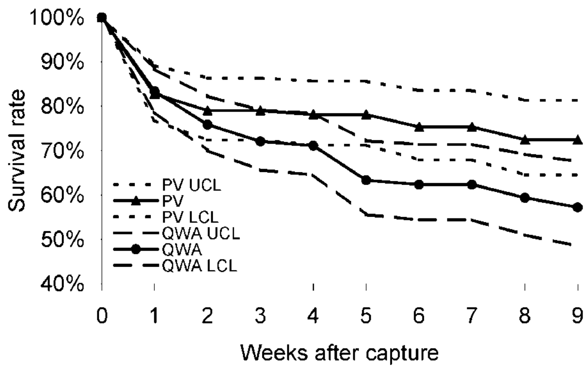

Figure 2. Survivorship functions and 95% log-normal confidence limits (PV = dotted lines, QWA = dashed lines) for 110 white-tailed deer fawns captured in an agricultural landscape (PV) and 108 fawns captured in a forested landscape (QWA), central Pennsylvania, 2000–2001.

1.16–1.94) for every 1 kg increase in capture mass.

Discussion

Survival

Nine-month survival rates of white-tailed deer fawns in central Pennsylvania approached 40% in a forested landscape with overbrowsed habitat conditions and presumed greater predator density, and exceeded 50% in an agricultural landscape with presumed lesser predator density. Survival at 26 weeks (180 days), a common benchmark of survival in other fawn studies, was 59% in PV and 46% in QWA. These survival rates were similar to published estimates of fawn survival in North America (Huegel et al. 1985, Nelson and Woolf 1987, Decker et al. 1992, Kunkel and Mech 1994, Long et al. 1998, Ballard et al. 1999).

Decker et al. (1992) observed one of the highest fawn-survival rates reported for any forested region: survival of 37 monitored fawns was 76% at 180 days in an extensively forested region in Massachusetts. Predation, poaching, and disease all were present, but Decker et al. (1992) suggested that greater survival was a function of good herd health, favorable winter weather, favorable habitat conditions, and reduced legal harvest rates. In regenerating and hardwood floodplain forests and adjacent hay and clover fields in New Brunswick, Ballard et al. (1999) monitored neonatal fawns to 180 days in late November; survival was 39.8%, and predation was the leading cause of mortality. In a nonhunted population on a coastal island in Maine where coyote predation was the leading cause of mortality, Long et al. (1998) observed a 6-month survival rate of 40% and annual survival of 26%. In Minnesota, Kunkel and Mech (1994) monitored fawns through October–November during 2 years when wolf (*Canis lupus*) and black bear predation were leading causes of mortality. Survival through this October–November period averaged 49%.

White-tailed deer fawn-survival estimates reported from agricultural landscapes in the central plains are comparable to those we estimated for PV. Nelson and Woolf (1987), working on a large mixed-forest and agricultural refuge in Illinois, reported "pre-hunt" (assumed to be approximately 6 months) survival rates from 62–79%. Huegel et al. (1985) monitored fawns to 180 days in an extensive agricultural landscape in Iowa and observed 73% survival.

Mortality causes

Predation. Predation was the leading cause of mortality in the extensively forested QWA (69.5%), where predator populations were assumed to be denser. In other forested regions, Decker et al. (1992) attributed 29% of mortalities to coyotes, and Long et al. (1998) and Ballard et al. (1999) attributed 47% and 41% of mortalities to coyotes, respectively. In New Brunswick, predation rates by coyotes, black bears, and bobcats were 10%, 18%, and 4%, respectively (Ballard et al. 1999). Rates of coyote predation we observed in PV (11%) were considerably lower than rates reported by 2 other fawn-survival studies in presumably similar agricultural landscapes. Huegel et al. (1985) in Iowa and Nelson and Woolf (1987) in Illinois observed coyote predation rates (proportion of fawn deaths attributed to coyote predation) in excess of 50%. The high predation rates we observed were consistent with other studies of fawn survival (Porath 1980, Linnell et al. 1995). Although proportion of fawn deaths attributed to coyote predation differed among regions where other fawn-survival studies were conducted, coyote predation was the leading cause of mortality in Massachusetts (Decker et al. 1992), Maine (Long et al. 1998), New Brunswick (Ballard et al. 1999), Illinois (Nelson and Woolf 1987), Iowa (Huegel et al. 1985), Texas (Cook et al. 1971, Carroll and Brown 1977), Mississippi (Bowman et al. 1998), and Oklahoma (Bartush and Lewis 1981). Percentage of mortalities attributed to coyotes in QWA in our study was <25%.

Black bear predation on free-ranging fawns has been documented in New York (Mathews and Porter 1988), New Brunswick (Ballard et al. 1999), and Minnesota (Kunkel and Mech 1994). Additional anecdotal information from Michigan (Ozoga and Verme 1982, Ozoga and Clute 1988), Vancouver (King 1967), and Alberta (Verspoor 1983) also suggests that black bears kill fawns. Verspoor (1983) suggested that black bears might kill fawns only when under excessive hunger stress. However, black bears accounted for 49% of mortalities of fawns in Minnesota where wolves accounted for 51% of mortalities (Kunkel and Mech 1994). In New Brunswick, Ballard et al. (1999) concluded that predation by black bears (23% of mortalities) was not different from predation by coyotes (41% of mortalities) during summer and autumn. In our study, black bear predation was statistically similar to coyote predation and both rates exceeded 31% of predation mortality. No other studies of white-tailed deer fawn survival with sample sizes similar to this study have documented significant predation of fawns by black bears.

Although bears and coyotes were the dominant predator species, bobcats also killed fawns. Bobcats were responsible for 3 mortalities within 34 weeks of capture, but we attributed no predation events in PV to bobcats. Bobcats also killed fawns in Massachusetts (Decker et al. 1992), New Brunswick (Ballard et al. 1999), Texas (Cook et al. 1971), Oklahoma (Bartush and Lewis 1981), and South Carolina (Epstein et al. 1983, 1985), but bobcat predation rates were low overall in all studies, including ours. Although domestic dogs and foxes are capable of killing fawns (O'Gara 1978), we attributed no predation events to dogs or foxes.

Natural causes, excluding predation. Natural causes, excluding predation, were the second leading cause of mortality (27%) overall and the leading causes of mortality in PV. Nearly 73% of starvation-related mortality occurred within 3 days of capture, suggesting that maternal abandonment because of handling may have been the underlying cause of these deaths. However, most fawns begin to ruminate at 14–20 days post-partum and are weaned by 5–10 weeks post-partum (Short 1964, Marchinton and Hirth 1984, Gauthier and Barrette 1985), so abandonment by a doe even at 30–60 days still might cause starvation- or malnutrition-related death that cannot be attributed to handling. In addition, Ozoga and Clute (1988: 550) reported that "many unmarked fawns apparently died when <2 days old." Furthermore, fawns may die within 3 days post-partum if the doe produces insufficient quantities of milk or dies. Because does in better habitats breed at younger ages than does in poorer habitats, and younger does are known to be less capable of caring for fawns (Cheatum and Severinghaus 1950, Verme 1977, Ozoga and Verme 1986), doe age and nutrition are closely related to fawn survival and may be more important than effects of handling in fawn-survival studies.

If we attributed all fawn mortalities from natural causes, excluding predation, within 7 days after capture to handling-related abandonment and consequently censored these mortalities, survival rates at 34 weeks would be 58.8% (95% CI=47.9–68.9%) in PV and 40.9% (95% CI = 30.0–52.8%) in QWA. However, we have no evidence to confirm or refute that fawn deaths from starvation or malnutrition were caused by abandonment after handling; therefore, we chose not to censor fawns dying from natural causes, excluding predation, within 7 days after capture.

Influence of sex, mass, and date of birth

Some evidence suggests that predation rates may be greater for males of sexually dimorphic species (Jackson et al. 1972, Owen-Smith 1993, Aanes and Andersen 1996). Because fawns are not dimorphic, Jackson et al. (1972) and Aanes and Andersen (1996) attributed greater predation rates of male white-tailed deer fawns and roe deer (*Capreolus capreolus*) fawns, respectively, to different activity patterns between males and females. However, sex of fawn was not an important explanatory variable in logistic regression or known-fate survival models in this study.

Fawn mass may be related to survival if heavier fawns are less susceptible to disease, starvation, or predation (Verme 1962, 1977; Guinness et al. 1978; Nelson and Woolf 1987; Kunkel and Mech 1994). If fawn mass and consequently individual fitness is less in areas with poor habitat conditions (e.g., overbrowsed forests on poor soils) than in areas where food is abundant (e.g., agricultural habitats), fawns in poor-quality habitats might be more vulnerable to predation and other mortality factors. Nelson and Woolf (1987) reported that fawns below the mean mass of fawns in their study at time of capture were more vulnerable to predation than fawns above mean mass at time of capture. Kunkel and Mech (1994) similarly concluded that predator-killed fawns weighed less than survivors. In our study, fawn mass at capture was not different between PV and QWA but was related to fawn survival at 9 weeks after capture in the best logistic regression model. However, survival models in program MARK determined that survival varied primarily over time, and models that included fawn mass at capture did not explain significantly more residual variation.

Statewide, 69.7% of all Pennsylvania fawns are born within 14 days of 1 June (PGC, unpublished data). This prey-swamping strategy likely overwhelms predator populations with an overabundance of prey (fawns) during a short time period (Edmunds 1974, Calow 1998). Therefore, individual fawns should be at reduced risk of predation during this period of fawn abundance. However, we were unable to detect a difference in survival rates between fawns captured farther from median annual fawn-drop date and fawns captured closer to peak drop date.

Influence of landscapes and habitat characteristics

Because deer are considered a species of edge or early-successional habitats, we hypothesized that survival would be greater for fawns having greater habitat patch diversity (SDI), more annual and perennial herbaceous habitats, and more edge habitats in home-range buffer areas. No characteristics of habitat composition and configuration in areas the size of fawn home ranges that we quantified were related to fawn survival within 9 weeks after capture. Because habitat patch diversity (SDI) was not related to fawn survival, either SDI was a poor measure of foraging opportunities or fawns and nursing does had sufficiently abundant, high-quality forage available, regardless of habitat diversity. Few 6-month-old does are bred in QWA (Rosenberry and Wallingford 2002), suggesting that poorer habitat conditions may exist there. Poor foraging quality may not be related to fawn survival if does reproduce only if they have the energy reserves to raise fawns. However, fawn starvation and malnutrition deaths in this study suggest that some does healthy enough to breed may not have had energy reserves to raise fawns.

Fawns with greater road densities in home-range areas should have a greater risk of vehicle collision. Roads also may serve as travel corridors for predators, hunters, and poachers. However, we failed to detect a relationship between road density within buffer areas and fawn survival.

Fawn home-range-scale habitat characteristics and landscape ecology may play an important role in fawn survival through habitat type and arrangement. For example, Stuart-Smith et al. (1997) observed greater caribou (*Rangifer tarandus caribou*) calf mortality and smaller home ranges in a fragmented landscape compared to an intact landscape, but reported no relationship between landscape configuration and caribou mortality. In a study of pheasant (*Phasianus colchicus*) nest success, Clark et al. (1999) concluded that habitat patch size, patch contagion, patch core area, distance to edges, and grassland edge density within one home-range radius were related to nest success. Thompson and Fritzell (1989) concluded that home-range size and mean daily movement were inversely related to ruffed grouse (*Bonasa umbellus*) survival rates. Conversely, Perkins et al. (1997) observed that pheasant survival was unrelated to small-scale habitat use and daily movements. Some evidence also suggests that predator home-range distribution, number and arrangement of predator territories on the landscape, and juxtaposition of predator and prey home ranges can influence predation rates (Rogers et al. 1980, Nelson and Mech 1981). Identifying specific landscape characteristics that influence fawn survival may be difficult because of availability of appropriate spatial and habitat data and, more importantly, separating potentially interactive effects of habitat, predators, doe age, and doe nutritional status.

Logistic regression and known-fate models identified differences in survival between study sites; however, we had no geographic replication of study landscapes. Therefore, we cannot infer that differences in fawn survival between PV and QWA were attributable to landscape condition or landscape-scale habitat characteristics (patch diversity, configuration, composition, juxtaposition, etc.). Also, we could not test whether habitat condition and predator densities interact to increase fawn-predation rates, but evidence for this exists (Carroll and Brown 1977, Huegel et al. 1985, Nelson and Woolf 1987, Long et al. 1998). Regardless, we believe poor habitat conditions and greater predator densities in QWA likely contributed to greater predation rates for fawns.

Our inability to detect habitat characteristics significantly related to fawn survival at the home-range scale may not be surprising, because white-tailed deer are habitat generalists. Other attempts to identify specific habitat characteristics important to deer are similarly inconclusive (Rothley 2001). This suggests that landscape-scale habitat characteristics (patch diversity, size, arrangement, juxtaposition) and other landscape characteristics (predator diversity, predator density) may be more important to fawn survival. Future studies of fawn survival should consider the landscape context through replicated studies of the relation between fawn survival and landscape composition and configuration.

Management implications

Because harvest statistics and population estimates indicate an increasing deer population during the last decade (Diefenbach et al. 1997, Anonymous 2002), Pennsylvania's deer population likely is still increasing. Therefore, we believe fawn deaths from predation, hunting, and poaching—causes of particular concern to hunters—are not preventing the deer population from growing.

Currently, the PGC uses a harvest-based model to estimate population size, but no field-based, empirical estimates of fawn survival or recruitment are used in the model (Diefenbach et al. 1997). Many state agencies also use deterministic models to estimate deer population size over time, but these models do not incorporate uncertainty parameter estimates (Shope 1978, Roseberry and Woolf 1991). However, population models that use multiple data sources and incorporate uncertainty using likelihood-based methods are available (White and Lubow 2002). Estimates of fawn survival, such as those presented here, can be incorporated into models to obtain likelihood-based estimates of population size.

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