

Final Report

EFFECTS OF HUNTER ACTIVITIES ON DEER MOVEMENTS AND HARVEST

Submitted by

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30 September 2008

EXECUTIVE SUMMARY

An estimated 932,000 white-tailed deer (*Odocoileus virginianus*) hunters in Pennsylvania added approximately \$476 million annually to the Commonwealth's economy through hunting-related expenditures in 2001. In addition, almost two million people expended approximately \$528 million to view, photograph, and feed deer, elk (*Cervus elaphus*), and black bear (*Ursus americanus*). Approximately one in twelve Pennsylvanians hunted deer in 2002.

An accurate estimate of harvest rate would help the Pennsylvania Game Commission (PGC) assess the potential effects of regulation changes. Changes in license allocation or season length are usually assumed to influence deer population dynamics through changes in harvest rates. However, deer management units with a spatially variable harvest rate may have refugia (areas with little or no deer harvest), which could mediate and possibly negate the effects of changes in antlerless allocations or season length.

To our knowledge, only one study (conducted in Minnesota) has examined the distribution of deer hunters and deer hunting mortality. A spatial model of the distribution of deer hunters and deer harvest in Pennsylvania could provide valuable information to natural resource managers and hunters alike.

The first objective of this study was to estimate annual survival and harvest rates of female white-tailed deer on both study areas and to evaluate whether hunting mortality rates varied spatially across each study area. The second objective was to model the spatial distribution of hunters across the landscape. The third objective was to use GPS collars to obtain intense location information (every hour) to monitor the movements of deer in response to hunter activities during the rifle deer hunting season.

Two study areas were selected that contained large tracts of public land primarily forested and managed by the Bureau of Forestry, Department of Conservation and Natural Resources and enrolled in the PGC's Deer Management Assistance Program. The study areas were located on and around the Sproul and Tuscarora state forests, in north-central and south-central Pennsylvania, respectively. Research was limited to public lands on both areas in 2005, but was expanded to private lands in 2006. These study areas were located in the two largest physiographic provinces in Pennsylvania that account for over 87% of the state's land area.

During 2005-2007, we captured 203 female deer on the Tuscarora study area and 200 deer on the Sproul study area. The 19 GPS radiocollars that were deployed to obtain detailed information on deer movements prior to and during the hunting season failed to work as designed. The manufacturer of the equipment was sold and its business was liquidated. Problems with the collars included battery failure, faulty release mechanisms, failure of electronic components in the collar, and poor signal strength that precluded remote download of data. We were able to monitor these deer for survival, but not enough locations were obtained to make inferences about the effect of hunter density and activities on deer movements. Therefore, we were not able to address this objective.

Hunting was the most common source of mortality for collared deer and most human-related mortalities (other than hunting) were vehicle collisions. Annual survival differed primarily by land ownership (public vs. private) and study area. On the Sproul study area annual survival was 90% on public land and 72% on private land. On the Tuscarora study area annual survival was 60% on public land and 79% on private land.

We found that some hunters were reluctant to harvest radiocollared deer even if it were legal to do so (PGC, unpublished data). Given such findings, it is possible that our sample of radiocollared deer may have resulted in underestimates of harvest rates. However, we note that an earlier study in Pennsylvania comparing harvest rates of male white-tailed deer fitted with ear-tag transmitters (that are difficult to see) and radiocollars exhibited no statistical difference in harvest rates (Long 2005, unpublished data). In light of how hunter behavior may have affected our estimates of harvest rates these estimates should be interpreted with caution. However, the results from this study are still valid for examining relative differences in harvest and hunting mortality (e.g., between study areas or land ownership) and in examining relationships between hunting mortality and landscape characteristics.

Harvest rates primarily differed between study areas, land ownership, and age class of deer. On the Sproul study area, the harvest rate was 5% on public lands and 18% on private lands. On the Tuscarora study area harvest rates were slightly lower on private land and differed between adults (20%) and juveniles (30%).

Other than evidence for greater harvest rates on public land, we found no landscape variables related to the spatial distribution of the harvest on the Tuscarora study area. On the Sproul study area we found greater harvest rates on private land. Furthermore, on public land, harvest rates declined for deer that lived further from roads and on steeper slopes. On private land, distance from road had little influence on harvest rates but deer that lived on steeper slopes tended to have lower harvest rates.

Hunter density was greatest during the first three days of the hunting season (0.5-1 hunter/km²) and then declined. Hunter density was generally ≤ 0.1 hunters/km² except on Saturdays. Deer hunting on Sunday is not permitted in Pennsylvania. On the Sproul study area we found that hunters were relatively uniformly distributed on private land. On public land there were large areas with relatively few hunters and most hunters were found on flat slopes near roads. On the Tuscarora study area, hunter density was greater on public lands, but overall there were only a few, small areas with relatively few hunters.

The distribution of hunting mortality on public land on the Sproul study area indicated large areas of land that experienced hunting mortality rates of $< 2\%$ and hunter distribution indicated low hunter density in these same areas. These areas of few hunters and low hunting mortality rates may serve as *de facto* refugia for deer. Thus, extended hunting seasons and increased number of DMAP permits could have minimal effect on

deer population dynamics. If so the only way to minimize the effect of refugia would be to increase hunter access to locations far from public roads and on steep slopes.

On private lands on both study areas we found a relatively uniform distribution of hunters. This is likely because use of vehicles was not regulated except by the landowner. As a result, on private lands we found no evidence for deer refugia on private lands. This would suggest that on private land, extended days of hunting and a greater number of licenses to harvest antlerless deer would likely increase the harvest rate on female deer.

Management of white-tailed deer populations by state wildlife agencies is applied to defined management units. These units usually are based on a combination of political boundaries, physical features of the landscape (e.g., roads, river, mountain ranges, etc.), and environmental characteristics (e.g., human population density, forest cover, etc.). Units typically are created to represent relatively uniform areas with respect to factors that influence deer populations. This research has found that potentially large differences in harvest rates occur within management units, but generalizations about differences between public and private lands are unlikely to be accurate. For example, in the Sproul study area we found that harvest rates of female deer were 4-6 times greater on private land, which is the opposite of what is commonly assumed by hunters. In contrast, on the Tuscarora study area we found evidence that harvest rates on public lands were slightly greater than on private lands.

State wildlife agencies must continue to manage deer across large management units because large areas are required to obtain sufficient data to monitor population and harvest trends. This research clearly shows that other tools (e.g., landowner specific permits to harvest deer) must be available to landowners (both public and private) to address deer population conditions in their local area.

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ACKNOWLEDGMENTS

We thank Dr. Duane R. Diefenbach, U.S. Geological Survey, Pennsylvania Cooperative Fish and Wildlife Research Unit at The Pennsylvania State University for his assistance with this project. Also, we greatly appreciate the Lehigh Valley Chapter of Safari Club International purchasing receivers for monitoring GPS collars.

INTRODUCTION

The white-tailed deer (*Odocoileus virginianus*) in North America has expanded its range over the last 100 years because of changes in land use caused by humans (Waller and Alverson 1997). By the turn of the 20th century, many state agencies began to enforce harvest regulations, resulting in deer density increases from approximately 2-8 deer/km² in pre-settlement times to present-day estimates averaging >11/km² and as high as 31/km² in areas of Pennsylvania (DeCalesta 1994, Diefenbach and Palmer 1997, Waller and Alverson 1997). At high densities, this dominant species is capable of changing forest vegetation structure, extirpating plant species, and adversely affecting other fauna, including songbirds, insects, and small mammals (DeCalesta 1994, Diefenbach et al. 1997, Waller and Alverson 1997).

In Pennsylvania, deer densities that adversely affect forest regeneration and bird abundance have been identified (DeCalesta 1994, Horsley et al. 2003). However, deer densities in the late 20th century were approximately twice what was recommended by biologists (Diefenbach and Palmer 1997, Diefenbach et al. 1997). In 2002, the Pennsylvania Game Commission (PGC) changed deer hunting regulations to create changes in age-sex structure and densities of the deer populations in most wildlife management units. The PGC instituted antler restrictions for bucks (at least 3 points on one antler required for harvest in most of the state, and 4 points required in a western region), increased the length of the antlerless season (and made it concurrent with all antlered seasons) and number of harvest permits for antlerless deer, and instituted a Deer Management Assistance Program (DMAP) to provide landowners additional antlerless harvest permits for their property.

An estimated 932,000 deer hunters in Pennsylvania added approximately \$476 million annually to the Commonwealth's economy through hunting-related expenditures in 2001 (U.S. Fish and Wildlife Service and U.S. Census Bureau 2003). In addition, almost two million people expended approximately \$528 million to view, photograph, and feed deer, elk (*Cervus elaphus*), and black bear (*Ursus americanus*). Approximately one in twelve Pennsylvanians hunted deer in 2002 (U.S. Fish and Wildlife Service and U.S. Census Bureau 2003, U.S. Census Bureau 2004). Many Pennsylvania deer hunters travel to a lodge or cabin with extended groups of friends or family, which demonstrates the tradition and social significance of deer hunting to many Pennsylvanians (Zinn 2003).

Harvest and Survival Rates

The harvest rate is the proportion of deer in a population that are legally killed and recovered by hunters. Hunters in Pennsylvania are required to obtain a license or permit to legally harvest a deer, and to report each harvest to the PGC via a mail-in report card (Rosenberry et al. 2004). The hunting mortality rate is the proportion of deer that are harvested, killed illegally during the hunting season, or fatally shot but not recovered (wounding loss). An estimate of hunting mortality helps biologists understand the effect of hunting on a population. One method of obtaining an estimate of harvest rate is to monitor a representative

sample of deer using radio-telemetry. Data on the timing and number of deer killed permit calculation of accurate estimates of the harvest rate (Heisey and Fuller 1985, Pollock et al. 1989).

Radio-telemetry studies have found that hunting represents the primary cause of mortality for deer (Dusek 1989, DelGiudice 2004). Hunting-related annual mortality rates of female white-tailed deer (averaged over the duration of the study) typically range from 10% (e.g., 13% in New Brunswick; Whitlaw et al. 1998) to 25% (e.g., 22% in Montana; Dusek et al. 1992). Lower hunting mortality rates (e.g., 4% in Michigan; Van Deelen et al. 1997) have been reported from locations with restrictive harvests of females. Fuller (1990) reported annual hunting mortality rates of 11.5% during rifle season, 2.3% during archery season, and 1.4% during muzzleloader season in north-central Minnesota.

Annual survival rates of white-tailed deer also have been studied throughout North America. Annual survival rates for hunted populations of adult female white-tailed deer averaged (over the course of each study) 66% to 78% (Dusek 1989; Fuller 1990; Dusek et al. 1992; Van Deelen et al. 1997). DelGiudice (2004) found that annual mortality was directly correlated with the number of antlerless deer licenses allocated.

An accurate estimate of harvest rate would help the PGC assess the potential effects of regulation changes. Changes in license allocation or season length are usually assumed to influence deer population dynamics through changes in harvest rates. However, deer management units with a spatially variable harvest rate may have refugia (areas with little or no deer harvest), which could mediate and possibly negate the effects of changes in antlerless allocations or season length.

In 2002, the PGC increased harvest opportunities for antlerless deer by providing additional permits to landowners through DMAP and by increasing the length of the antlerless rifle season. Because the Sproul and Tuscarora state forests were enrolled in DMAP in 2005 and 2006, harvest estimates of these study areas would provide insight to the effectiveness of this program. These harvest data also will help natural resource managers and concerned hunters understand the effect of hunting on Pennsylvania's deer herd.

Hunter Density and Distribution

To our knowledge, only two studies have estimated spatial variation in hunters. Broseth and Pederson (2000) found that harvest of willow ptarmigan (*Lagopus lagopus*) was predicted by hunting pressure modeled as a function of distance from a hunting camp. Fuller (1990) found that deer hunter density decreased with distance to road. Other studies have compared harvest rates of white-tailed deer on study areas with different habitat features such as forage type and quantity, dominant tree species, patch size of clearcuts, kilometers of roads, and number of hunters (Kammemeyer and Moser 1990, Dusek et al. 1992).

Existing literature on hunter density and distribution is largely limited to research conducted by Stedman et al. (2004) and Diefenbach et al. (2005) on public land in north-central Pennsylvania. Both studies recorded hunter locations via aerial surveys and statistically modeled hunter distribution as a function of landscape features. More hunters were found on flat slopes and close to roads during both studies. The authors used distance sampling methods (Buckland et al. 2001) to estimate maximum hunter densities of 0.2–0.7 hunters/km². However, adverse weather conditions restricted data collection to the hours of 10:00 am – 12:00 pm on opening morning in 2001, and postponed research until the second day of rifle season in 2002. Maximum hunter densities are likely greatest opening morning of the regular rifle season in Pennsylvania because this is the day of greatest harvest (PGC, unpublished data). Fuller (1988) estimated a maximum hunter density of 2.5 hunters/km² on opening morning in northern Minnesota.

Diefenbach et al. (2005) concluded that hunters were not distributed evenly across the landscape, but rather selected flat locations close to roads. Only 56% of the study area was located within 0.5 km of a road yet 87% of hunters were found within that distance. Hunters also were 1.5 times less likely to hunt a given location for every 5 degree increase in slope of the landscape. Fuller (1988) reported that 98% of all hunters in a study area in northern Minnesota, USA were located within 0.8 km of roads, which represented 50% of the study area. Other research has reported uneven distributions of elk and willow ptarmigan hunters (Broseth and Pedersen 2000, Millspaugh et al. 2000).

An uneven distribution of deer hunters may create areas of refugia on the landscape that experience little or no hunting pressure. Source-sink dynamics observed on such landscapes can serve to maintain or increase population numbers, even if adjacent areas are heavily hunted (Joshi and Gadgil 1991, Brown et al. 2000, Novaro et al. 2000, Siren et al. 2004). Population control in such a system may require hunter penetration into the refugia, as opposed to increase harvest on the hunted portions. Brown et al. (2000) concluded that several areas in New York, USA that contain refugia do not maintain adequate hunting pressure to keep deer herds in check. An understanding of where on the landscape these refugia exist would help landowners and biologists manage deer populations by identifying where hunters need better access.

Other research on hunter density and distribution is of limited relevance to this project. Millspaugh et al. (2000) estimated a utilization distribution of elk hunters on a strictly controlled hunt in South Dakota, and Thomas et al. (1976) examined the influence of forestland characteristics on deer, turkey, and squirrel hunters in West Virginia; both studies relied largely on hunter-reported location details. Hunter surveys conducted by Stedman et al. (2004) compared hunter-reported location information to data logs recorded on GPS units carried by hunters. Inaccuracies of the self-reported location data demonstrated the limited value of such information. Broseth and Pedersen (2000) used GPS units to record movement patterns of 9 willow ptarmigan hunters and estimate the distribution of hunting pressure over 50 days.

The research conducted by Diefenbach et al. (2005) and Stedman et al. (2004) provides a foundation of proven methods and base-line information for comparison to this study. However, their results probably lacked estimates of maximum hunter density because of the inability to fly the opening hunting hours of either study year. Additionally, their limited study area did not address potential differences in hunter density or distribution on private land or in other regions of the state. Furthermore, Diefenbach et al. (2005) had no information on how the distribution of hunters might be related to where deer were harvested.

Hunter Distribution and Deer Harvest

Wildlife management agencies, such as the PGC, use harvest data to estimate deer populations and allocate hunting licenses. Because these harvest data only estimate abundance on hunted portions of the landscape, deer density on refugia would remain unknown. An understanding of hunter distribution and its relationship to harvest rate could help the agency improve population estimation methods.

The distribution of harvest and hunters has been given little consideration in deer management. However, if landscape features influence the distribution of hunters and create refugia where deer harvest is low, then managers that rely primarily on data from harvested deer to monitor the population would not necessarily detect the presence of refugia. When refugia are present, managers might need to either increase harvest rates of the hunted portion of the deer population or increase hunter penetration to increase the harvest rate of the overall population. In such areas, activities such as opening and maintaining roads or allowing ATV access may be more effective than increasing license allocations or season length.

To our knowledge, only one study has examined the distribution of deer hunters and deer hunting mortality. Fuller (1988) found that deer hunter density and hunting mortality rate decreased with each of three increasing distance to road categories. Broseth and Pedersen (2000) conducted similar research on willow ptarmigan and found that harvest decreased with increasing distance from a base camp. A statistical model of the spatial distribution of doe harvest on the Sproul and Tuscarora landscapes could provide valuable information to natural resource managers and hunters alike.

Pennsylvania deer hunting seasons included archery, muzzleloader, regular rifle, and flintlock-only in 2005–2007. Because hunter participation is historically greatest during the regular rifle season (28 November–10 December 2005, 4–16 December 2006, and 26 November–8 December 2007), we limited our research on hunter density and distribution to these dates. The first objective of this study was to estimate annual survival and harvest rates of female white-tailed deer on both study areas and to see if hunting mortality rates varied spatially across each study area. The second objective was to model the spatial distribution of hunters across the landscape.

STUDY AREAS

Two study areas were selected that contained large tracts of public land primarily forested and managed by the Bureau of Forestry, Department of Conservation and Natural Resources and enrolled in the PGC's Deer Management Assistance Program (DMAP). The study areas were located on and around the Sproul and Tuscarora state forests, in north-central and south-central Pennsylvania, respectively (Figure 1). Research was limited to public lands on both areas in 2005, but was expanded to private lands in 2006. These study areas were located in the two largest physiographic provinces in Pennsylvania that account for over 87% of the state's land area.

Sproul Study Area

The Sproul study area was located within Wildlife Management Unit (WMU) 2G, which is largely contiguous forest in north-central Pennsylvania in the Appalachian Plateau physiographic province. The landscape in WMU 2G is 90% forested and contains 49% public lands. The forest is in the transition zone of the mixed-oak hardwoods and northern hardwoods. Annual snowfall at the Renovo, Pennsylvania weather station averaged 28.1 inches from 1971-2000 (National Oceanic and Atmospheric Administration 2004). Deer productivity is relatively low with 137 embryos per 100 adult does and 6 % of fawns pregnant (PGC, unpublished data).

In 2005, the Sproul study area encompassed 40,619 hectares, 72% of which was located within the boundaries of the Sproul State Forest (Figure 2). An additional 19% of the study area encompassed State Game Lands 100 and 9% of the study area was privately owned. Most of the road network open to the general public was located on the flat plateaus at the highest elevations. These plateaus were dissected by steep river drainages of the West Branch of the Susquehanna River.

In 2006, the boundaries of the Sproul study area were extended to the south and west to include an additional 29,074 ha of nearly all privately-owned land, except for SGL 100 and SGL 78. The private lands added in 2006 included a large road network. Privately-owned land comprised 46% of the total study area in 2006.

Tuscarora Study Area

The Tuscarora study area was located within WMU 4B, which was located in the Ridge and Valley physiographic province. This WMU is 64% forested but only 15% is public land. The ridges support a mixed-oak hardwood forest and the valleys support farmland and human developments. Annual snowfall at the Bloersville, Pennsylvania weather station averaged 21.2 inches from 1971-2000 (National Oceanic and Atmospheric Administration 2004). Deer productivity is greater than on the Sproul study area with 170 embryos per adult doe and 22% of fawns pregnant (PGC, unpublished data).

In 2005, the Tuscarora study area encompassed 27,672 hectares: 52% public land and 48% private land (Figure 3). The public land included the forested ridges of the Tuscarora State Forest. The road network on the Tuscarora State Forest traversed the ridges and valleys.

In 2006, the study area was expanded to include an additional area of 35,544 ha approximately 40 km to the east. This extension of the Tuscarora study area contained 88% private lands; the remaining 12% of the landscape was composed of State Game Lands 170, 230, 256, and 281. Privately-owned lands comprised 71% of the total study area in 2006.

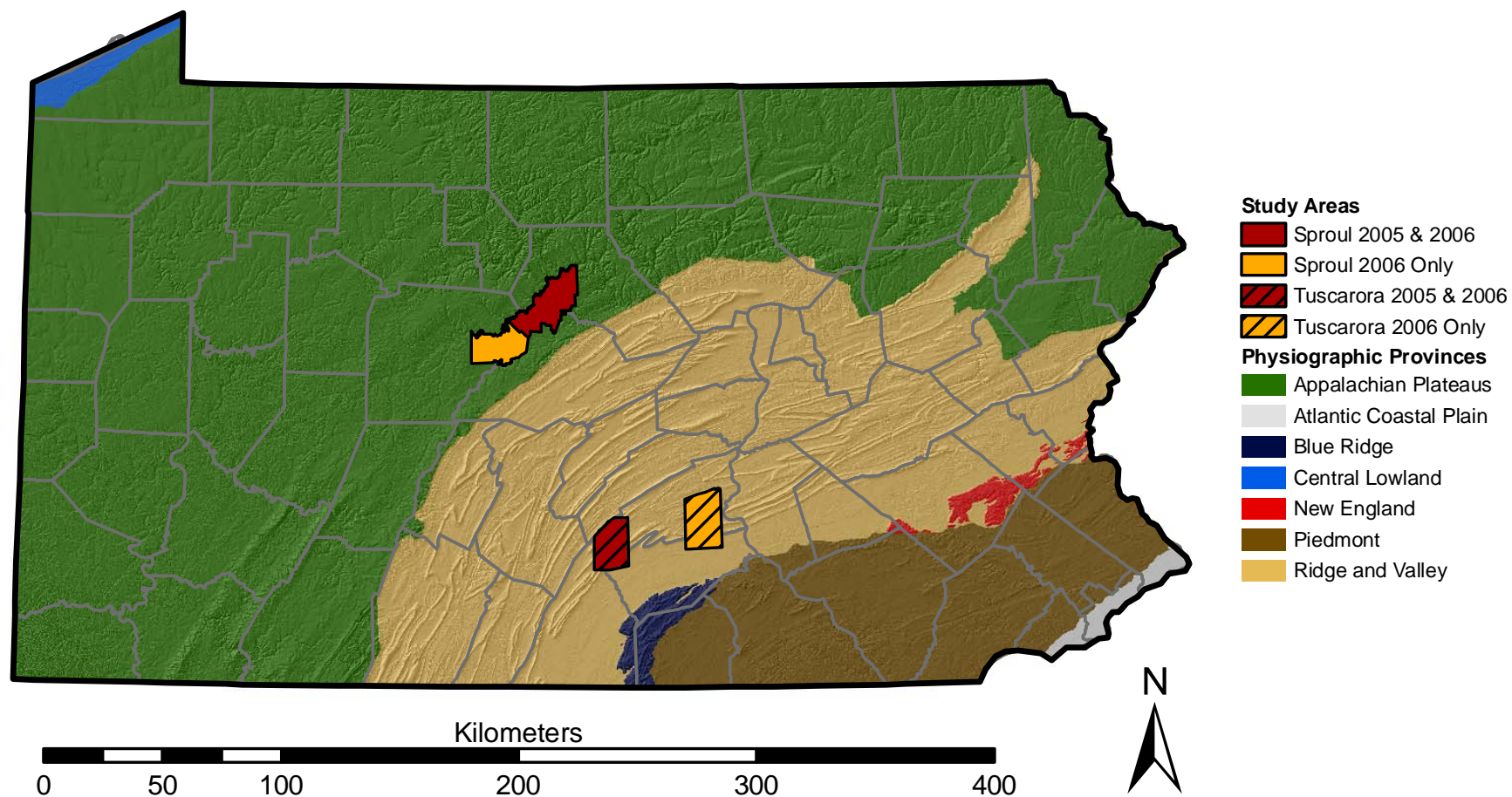


Figure 1. Location of the Sproul and Tuscarora study areas. In 2005, deer capture was restricted to mostly public lands on the areas colored in red. In 2006, more deer captures occurred on privately-owned land in the expanded study area.

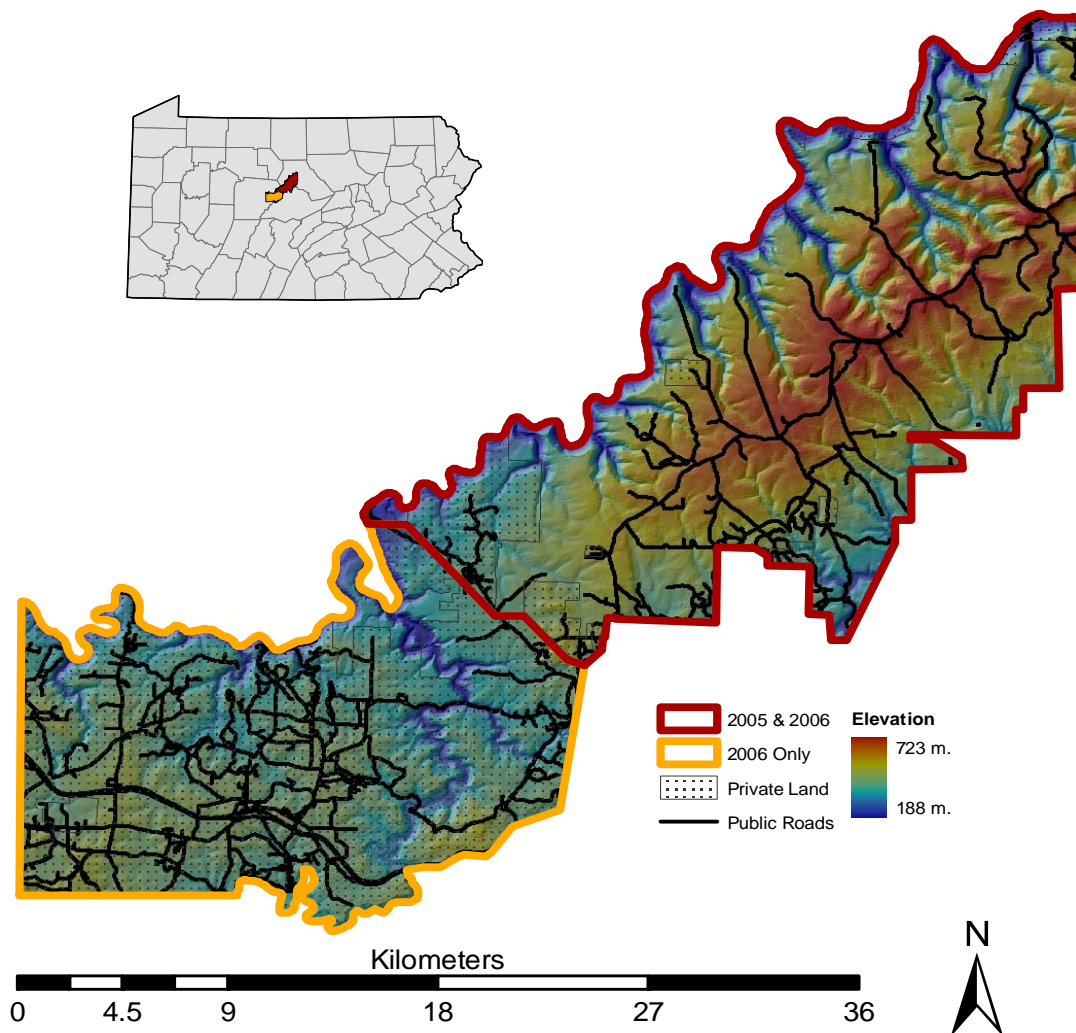


Figure 2. The Sproul study area, located in north-central Pennsylvania in the Allegheny Plateau (elevation in meters). The section outlined in orange was added in 2006. Gray stipples indicate private land ownership.

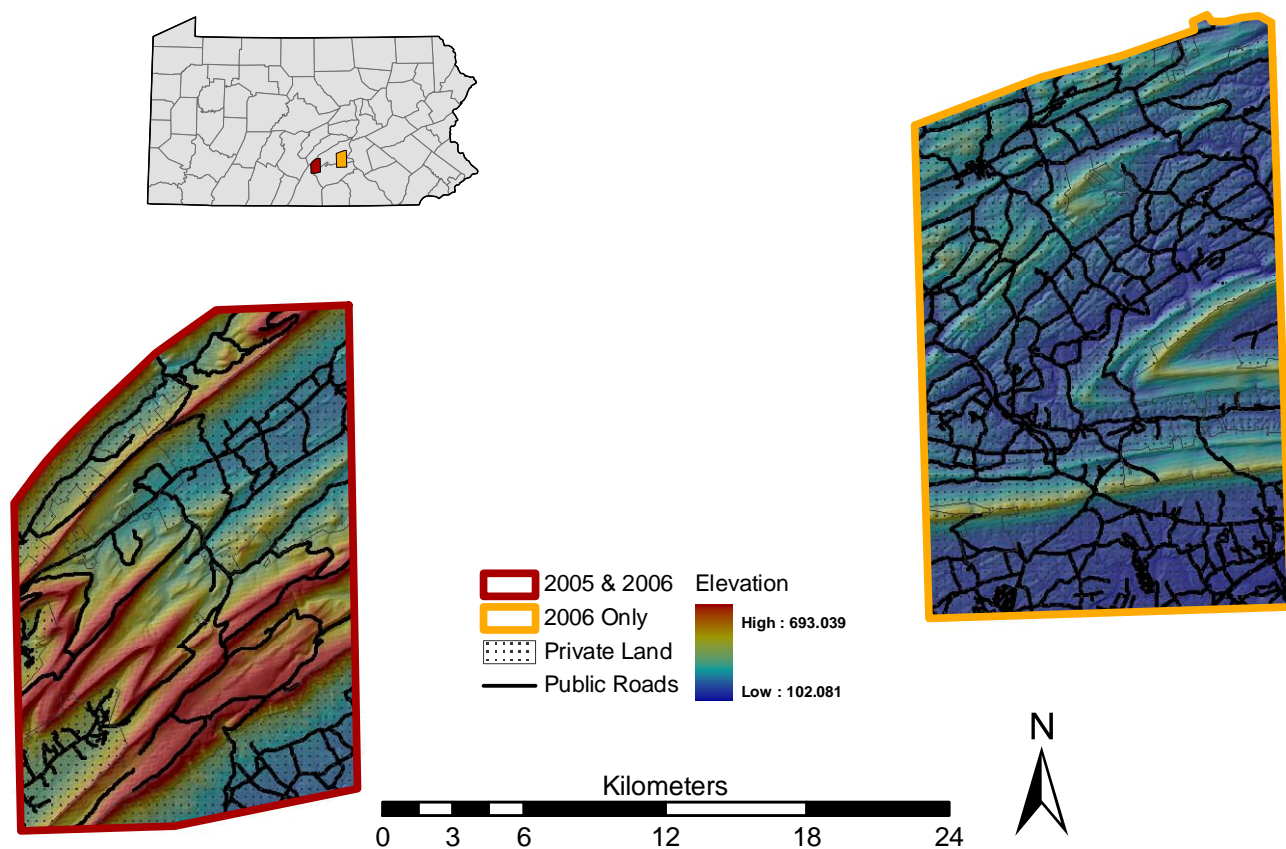


Figure 3. The Tuscarora study area, located in south-central Pennsylvania in the Ridge and Valley Province (elevation in meters). The section outlined in orange was added in 2006. Gray stipples indicate private land ownership.

METHODS

Capture and Marking of Deer

We captured deer January - April of 2005, 2006, and 2007 using modified Clover traps, drop nets, and rocket nets. In August 2006, we used chemical capture equipment (Dan-Inject of North America, Fort Collins, Colorado, USA) to re-deploy 1 GPS collar that was recovered prior to the hunting season. All deer were handled in accordance with protocols approved by the Pennsylvania State University Institutional Animal Care and Use Committee (IACUC Nos. 19909 and 26886).

Corn was the typical bait, although apples, alfalfa, and sweetened feed (a mixture of molasses, grains, and minerals) also were used. We set Clover traps close to roads accessible by 4WD vehicles and checked them daily for captures. We installed drop nets in fields and forest openings larger than 40 m × 40 m. Rocket nets were placed in openings larger than 15 m × 20 m. Deer captured in Clover traps were physically restrained, ear tagged, and radio-collared in <5 minutes. Deer captured in drop or rocket nets were sedated with xylazine hydrochloride intramuscularly at approximately 0.6 mg/kg body weight. Prior to release, we administered tolazoline hydrochloride intramuscularly at approximately 4.0 mg/kg body weight to reverse the effects of the sedative.

We blindfolded all captured deer during handling to reduce stress to the deer and attached a uniquely numbered tag in each ear (Original Tags, Temple Tags Co., Temple, Texas, USA). Juvenile females were fitted with either a 260 g VHF neck collar (Advanced Telemetry Systems, Inc., Isanti, MN, USA), or a 700 g GPS neck collar (Telonics, Inc., Mesa, AZ, USA). Adult females were fitted with either of the same transmitter types or a 1,100 g GPS neck collar (Advanced Telemetry Systems, Inc., Isanti, Minnesota, USA). In 2007, on adult and juvenile females, we deployed 19 GPS collars designed with a UHF remote download of location data (Habit Research, Victoria, British Columbia, Canada). All deer were released at the capture location.

Determining Causes of Mortality

During the capture season, we classified deaths occurring within 2 weeks of capture as capture myopathy and data from these deer were not included for data analysis. However, one exception was that we classified mortalities occurring >1 week after capture as starvation if little fat existed in bone marrow of the femur (Depperschmidt et al. 1987, Van Deelen et al. 1997, Bender et al. 2004) and no evidence of predation existed. Another exception was that if a deer were found dead <100 m from a road, regardless of time since capture, we classified it as road-killed if it showed evidence of physical trauma consistent with a vehicle collision.

The VHF and GPS collars included circuitry to detect lack of movement and transmit a different signal to indicate the deer may have died. Also, VHF collars were equipped with a

precise event transmitter (PET) that transmitted a signal indicating the time elapsed since the collar entered mortality mode. We monitored all deer for survival once per week during the capture period, and twice per week the remainder of the year.

Mortalities were investigated as soon as possible, and we used field necropsy methods used to identify cause of death (Adrian 1996, Vreeland 2002, Bender et al. 2004). We submitted carcasses to the Pennsylvania State University, Animal Diagnostic Laboratory for necropsy if cause of death could not be determined in the field.

To facilitate hunter reporting of harvested deer, ear-tags and transmitter collars were labeled with a toll-free telephone number. Also, we posted signs throughout both study areas indicating radio-collared deer were legal for harvest and instructing hunters to report harvested deer. Personal communication with hunters, however, suggested that some hunters were uncooperative and would discard or destroy the radio-collar. Therefore, deer that we lost contact via telemetry during the hunting seasons, and were not found after subsequent ground and aerial searches, were assumed to be legally harvested. Also, we assumed radio-collars found with the collar cut and abandoned during a hunting season were legally harvested. If evidence indicated deer were killed outside a hunting season, or outside legal hunting hours, we classified them as illegally killed.

Locating Radio-collared Deer

We attempted to estimate the location of each VHF radio-collared female deer twice per week May-December 2005-2007 using ground telemetry triangulation. We used program LOAS v. 2.10 (Location of a Signal, Ecological Software Solutions, Sacramento, CA, USA) to estimate each deer location using the Andrews-M estimator. We tried to ensure the 95% error ellipse of each locations was <1 ha. If we located a collared deer visually, we recorded our location and the bearing and distance to the deer and used trigonometry to calculate the location of the deer. GPS collars were programmed to estimate and store the deer's location on-board once every 23 hours from date of capture until 15 September, at which point the frequency of fixes increased to once per hour. Depending on the model, GPS collars either were pre-programmed to release on 15 January of each year, or they were sent a release command from a VHF command unit on approximately the same date. The GPS radio-collars deployed in 2007 were programmed to release in January 2009.

Aerial Surveys of Hunters

To estimate hunter density during the regular rifle season of 2005-2007, we used aerial surveys to locate hunters and distance sampling methods to estimate hunter density (Diefenbach et al. 2005). For the 2005 and 2006 data we used resource selection functions to model hunter distribution (Stedman et al. 2004, Diefenbach et al. 2005). We used two observers to locate hunters from fixed-wing aircraft navigating pre-defined transects. Transects were systematically placed over the study area from a random starting point and

oriented in the east-west direction. In 2005, 15 transect lines totaling 22.8 km and 16 transect lines totaling 21.1 km were defined for the Sproul and Tuscarora study areas, respectively. Two flights per day were conducted on each study area during the regular rifle season, weather permitting. Morning flights occurred between 0800 and 1100, and afternoon flights from 1330 to 1630. Pilots could safely navigate >225 m above the high plateaus of the Sproul study area, but were forced to remain >525 m above the ridge-and-valley topography of the Tuscarora study area; both maintained airspeeds of approximately 190 km/hr (~100 knots).

We provided each observer with a tablet PC (Hammerhead, DRS Tactical Systems, Melbourne, FL, USA) running geographic information system software (ArcGIS, Environmental Systems Research Institute, Redlands, CA, USA) that displayed a 3-dimensional view of the landscape (as well as roads and streams) in real time as seen by the observer. Locations of hunters were plotted by the observer directly on the GIS using a digitizing pen. In addition, the flight path of the plane was recorded.

Estimating Annual Survival

We estimated annual survival using the Kaplan-Meier known fates method implemented in Program MARK (White and Burnham 1999). The models incorporated weekly fate data from 1 May 2005 – 30 April 2006 (study year 2005), 30 April 2006 – 29 April 2007 (study year 2006), and 25 April 2007 – 16 April 2008. Deer that died or were censored between the date of capture and the start of this survival period were not included in the analysis. We considered models with several temporal (Table 1) and group (Table 2) effects.

After separately modeling all combinations of temporal and group effects, we estimated a 95% confidence set of models using methods outlined in Burnham and Anderson (2002). Starting with the model with the lowest value of Akaike's Information Criterion corrected for sample size (AICc), models with increasingly larger AICc values were added to the 95% confidence set of models, and a model weight, w_i , was calculated for each model in the set (Burnham and Anderson 2002),

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{r=1}^R \exp\left(-\frac{1}{2}\Delta_r\right)},$$

where Δ_i is the difference in AIC between model i and the model with the lowest AIC. Each time a model was added, the weights of all models in the set were summed, until the sum was ≥ 0.95 .

Table 1. Temporal models considered in annual survival analysis of antlerless deer on Sproul and Tuscarora study areas, Pennsylvania, USA 2005-2007.

Temporal models	Description
S(.)	No time effect - survival constant through time.
S(month)	Survival varies by month
S (Hunt; NoHunt)	Survival is constant during all hunting seasons (rifle, archery, muzzleloader), and constant outside of hunting season
S (Rifle; A/M; NoHunt)	Survival is constant during rifle season, constant through archery/muzzleloader seasons, and constant outside of hunting seasons
S (Rifle; NoRifle)	Survival is constant during rifle season, and constant through all other weeks of the year
S(Rifle; A/M; Fall; Wntr; Sumr)	Survival is constant during rifle season, constant through all archery and muzzleloader seasons, constant through non-hunting weeks from 1 October-15 January (Fall), constant from 15 January – 30 April (Winter), and constant from 1 May–29 September (Summer)

Also, we estimated survival rates for adults and juveniles (AGE), and for deer that lived on public land and private land (OWNER; Table 3). We classified captured deer <1 year old as juveniles and all older deer as adults. We classified a deer as living on private or public land when >50% of locations occurred on the given ownership type.

For the selected model set described heretofore, we created additional models that included the variables from Table 3 and created a 95% confidence set. We used these models to calculate a model-averaged survival estimate (Burnham and Anderson 2002),

$$\hat{S} = \sum_{i=1}^R w_i \hat{S}_i,$$

where \hat{S}_i = estimated survival from model i . The associated variance was calculated as

$$\text{var}(\hat{S}) = \left[\sum_{i=1}^R w_i \sqrt{\text{var}(\hat{S}_i | g_i)} + (\hat{S}_i - \hat{S})^2 \right]^2$$

and a 95% confidence interval as

Table 2. Study area (Site) and year (Yr) model configurations to estimate annual survival rates of antlerless deer on the Sproul and Tuscarora study areas, Pennsylvania, USA 2005-2006.

Group variable	Description
*Site	Survival is different on each study site
*Yr	Survival is different during each year.
*Site*Yr	Survival is different for each combination of study site and year.
+Site	The study site has an additive effect on survival (survival function for Sproul has the same slope but different intercept than that for Tuscarora).
+Yr	Year has an additive effect on survival (survival function for 2005 has the same slope but different intercept than that for 2006).
+Site +Yr	Study site and year both have additive effects on survival (survival function has the same slope for all study areas and years, but intercepts are different for 2005 than for 2006, and different for Sproul than for Tuscarora).
+Site *Yr	The study site has an additive effect on survival; survival is different for each year (survival function has a different slope for 2005 than for 2006, and a different intercept for Sproul than for Tuscarora).
+Yr *Site	The year has an additive effect on survival; survival is different for each study area (survival function has a different slope for Sproul than for Tuscarora, and a different intercept for 2005 than for 2006).

$$95\% \text{ CI} = (\hat{S} / C, \hat{S} * C),$$

$$\text{where } C = \exp \left[z_{\alpha/2} \sqrt{\ln(1 + [cv(\hat{S})]^2)} \right] \text{ and } cv(\hat{S}) = se(\hat{S}) / \hat{S}.$$

For 2007 data, we estimated the annual survival rate by 30-day intervals from 25 April 2007 through 16 April 2008. We developed models that included study area, age (juvenile, adult), and time and used survival rate estimates from the model with the lowest AICc value. We calculated 95% confidence intervals as described for 2005-2006 data.

Table 3. Variables included in models of female white-tailed deer annual survival on the Sproul and Tuscarora study areas, Pennsylvania, USA 2005-06.

Variable	Description
AGE	Survival varies between adults and juveniles.
OWNER	Survival varies between deer on public and private land.
OWNER*Site	The effect of land ownership on deer survival is different on Sproul than it is on Tuscarora.
AGE, OWNER	Survival is different between adults and juveniles, and between deer on public and private land.
AGE, OWNER*Site	Survival varies between adults and juveniles; the effect of land ownership on survival is different on Sproul than it is on Tuscarora.

Estimating Harvest Rate

For 2005-2006 data, we estimated the harvest rate on each study area using the known-fates procedure in Program MARK for the 12-week hunting season. Only harvests (deer shot and recovered) were entered as deaths in the encounter history and all other mortalities were treated as censored deer. We developed several temporal harvest rate models (Table 4), and identified a 95% confidence model set. We then included the variables of AGE and OWNER and identified a second 95% confidence set of models. We model-averaged the harvest rate and estimated standard errors and 95% confidence intervals using the methods described heretofore for annual survival.

For 2007 data, we estimated the harvest rate for the hunting season by two-week intervals from 21 September 2007 through 24 January 2008. We developed models that included study area, age (juvenile, adult), and time and selected the model with the lowest AICc value.

Table 4. Temporal models evaluated to estimate harvest rate of female white-tailed deer on the Sproul and Tuscarora study areas, Pennsylvania, USA 2005-06.

Model name	Description
H (.)	No time effect - hunting mortality is constant through hunting seasons and years
H (Year)	Hunting mortality rate varies between 2005 and 2006, but is constant within each year.
H (Week)	Hunting mortality rate varies by week, but is the same in 2005 and 2006.
H (Week*Year)	Hunting mortality rate is different for every week in both 2005 and 2006.
H (Week+Year)	Hunting mortality rate varies by week. The mortality function in 2005 has the same slope, but different intercept than that for 2006.
H (Rifle; A/M)	Hunting mortality rate is constant during the rifle season and constant during archery and muzzleloader seasons, with no differences between years.
H (Rifle; A/M * Year)	Hunting mortality rate is constant during the rifle season and constant during archery and muzzleloader seasons, with a unique mortality function for 2005 and 2006.
H (Rifle; A/M + Year)	Hunting mortality rate is constant during the rifle season and constant during archery and muzzleloader seasons. The mortality function in 2005 has the same slope, but different intercept than that for 2006.

Spatial Modeling of Hunting Mortality

We modeled hunting mortality, K , as a function of various landscape variables, including the distance from the nearest road (ROAD), the slope of the landscape (SLOPE), and land ownership (OWNER) for the 2005 and 2006 data. In addition to harvested deer, we included deer not recovered by hunters to model the probability that a deer died as a result of hunting. We created a grid for each study area with 30 m \times 30 m cells containing values for these three landscape variables. We calculated ROAD as the linear distance from the center of each cell to the nearest road open to public travel during the hunting season. The road layer contained state forest roads, as well as municipal and state-maintained roads. We calculated slope with the Spatial Analyst extension in ArcMap, from a 26 m \times 26 m digital elevation model (National Elevation Dataset, U.S. Geological Survey) so that the slope value for each cell was the average of each grid cell and the 8 neighboring grid cells. Each cell was assigned an OWNER value of 1 if the center-point fell within state forest or state game land boundaries and 0 otherwise.

We linked the values of distance to road, land ownership, and slope to the last 30 telemetry locations for each deer. To ensure that this sample of locations was representative of the deer's location during the hunting season (when it was vulnerable to harvest), we visually examined each location in the GIS to detect shifts in spatial location or use of the three variables (ROAD, SLOPE, OWNER). If we detected a shift in locations of the deer, we excluded all locations prior to the shift.

We estimated hunting mortality using the Kaplan-Meier known fate method in Program MARK for each study area. All hunting mortalities (recovered and unrecovered hunter kill) were counted as deaths and all other mortalities were censored. In addition to the variables considered in the models in Tables 5 and 6, we included a year effect (2005 and 2006). We used the logit link to model harvest rate as a function of ROAD, SLOPE, and OWNER.

We identified a 95% confidence set of models and model averaged each coefficient term, $\hat{\beta}_{j,i}$ (coefficient for predictor j in model i)

$$\tilde{\beta} = \sum_{i=1}^R w_i I_j(g_i) \hat{\beta}_{j,i},$$

where $\hat{\beta}_{j,i}$ = estimated coefficient for predictor x_j in model g_i , and $I_j(g_i) = 1$ if predictor x_j is in model g_i , 0 otherwise. The variance of this model-averaged coefficient was estimated as

$$\text{var}(\tilde{\beta}) = \left[\sum_{i=1}^R w_i \sqrt{\text{var}(\hat{\beta}_i | g_i)} + (\hat{\beta}_i - \tilde{\beta})^2 \right]^2.$$

Coefficients for each variable were estimated using a logit-link function and used to predict the probability of hunting mortality across the landscape, such that

$$\hat{K} = 1 - \left[\frac{e^{\tilde{\beta}_0 + \sum x_p \tilde{\beta}_k}}{1 + e^{\tilde{\beta}_0 + \sum x_p \tilde{\beta}_k}} \right],$$

where the x_p are the variables used in the selected model set and the $\hat{\beta}_k$ are the estimated model-averaged coefficients for the predictor variables.

Hunting mortality was estimated for each 30 m x 30 m grid cell and mortality values were displayed on a map as a color gradient, with lighter colors representing greater hunting mortality rates and darker colors representing areas with lower hunting mortality rates.

Table 5. Temporal models considered in spatial variation in the hunting mortality rate of female white-tailed deer on the Sproul and Tuscarora study areas, Pennsylvania, USA 2005-06.

Model name	Description
M (.)	No time effect - hunting mortality is constant through hunting seasons and years
M (Year)	Hunting mortality rate varies between 2005 and 2006, but is constant within each year.
M (Week)	Hunting mortality rate varies by week, but is the same in 2005 and 2006.
M (Week*Year)	Hunting mortality rate is different for every week in both 2005 and 2006.
M (Week+Year)	Hunting mortality rate varies by week. The mortality function in 2005 has the same slope, but different intercept than that for 2006.
M (Rifle; A/M)	Hunting mortality rate is constant during the rifle season and constant during archery and muzzleloader seasons, with no differences between years.
M (Rifle; A/M * Year)	Hunting mortality rate constant during the rifle season and constant during archery and muzzleloader seasons, with a unique mortality function for 2005 and 2006.
M (Rifle; A/M +Year)	Hunting mortality rate constant during the rifle season and constant during archery and muzzleloader seasons. The mortality function in 2005 has the same slope, but different intercept than that for 2006.

Table 6. Variables use in model of hunting mortality of female white-tailed deer on the Sproul and Tuscarora study areas, Pennsylvania, USA 2005-06.

Variable name	Description
AGE	Age of the deer (juvenile vs. adult)
ROAD	Distance from the nearest road (m)
SLOPE	Slope of the landscape (degrees)
OWNER	Land ownership (public, private)
ROAD ²	Squared distance from the nearest road (m ²)
SLOPE ²	Squared slope of the landscape (degrees ²)
ROAD*SLOPE	Interaction between distance and slope
ROAD*OWNER	Interaction between distance and land ownership
SLOPE*OWNER	Interaction between slope and land ownership
ROAD*SLOPE*OWNER	Three-way interaction among ROAD, SLOPE, and OWNER

Estimating Hunter Density

We estimated hunter density using distance sampling methods in program DISTANCE (Buckland et al. 2001, Stedman et al. 2004, Diefenbach et al. 2005, Thomas et al. 2006). We estimated detection functions for each observer based on the perpendicular distance between observed hunters and the flight path of the aircraft. Because the location of aircraft windows precluded viewing directly below the aircraft, observers were unable to detect hunters close to the flight path. To adjust for this problem, we examined a histogram of observations of hunters by distance from the flight path and for each observer. We identified a distance at which hunters were not likely to be obscured and assigned this as zero distance and assumed all hunters were detected at this distance, but not necessarily at greater distances.

In 2005 we surveyed only public land (Figure 2 and 3) but in 2006 we estimated hunter density separately for public and private land. We classified a transect line as “public” if >50% of the land within the estimated survey strip width were publicly owned. We post-stratified the data by each survey flight to estimate hunter density for each by flight. We modeled the detection function by observer using data from all flights and applied this detection function to estimate hunter density for each flight. Half-normal and hazard-rate functions were considered for all models and selected the model with the lowest AICc value.

Spatial Modeling of Hunter Distribution

We modeled hunter distribution with respect to the same landscape variables as hunting mortality (Table 7, see *Spatial Modeling of Hunting Mortality*). Locations where hunters were observed were overlaid the grid and associated grid cells were classified as used habitat by hunters. We randomly selected 10,000 cells from the study area and classified these as a sample of available habitat. Resource selection by hunters was estimated for each year and study area using logistic regression methods (Manly et al. 2002, Stedman et al. 2004, Diefenbach et al. 2005), where the model predicted that a grid cell was used by hunters. We used PROC LOGISTIC in SAS software (SAS Institute, Cary, North Carolina, USA) and a 95% confidence set of models to estimate model-averaged coefficients for the logistic model (see *Spatial Modeling of Hunting Mortality*).

We used the model-averaged coefficients to develop a resource selection function (RSF, Manly et al. 2002),

$$RSF = \frac{e^{\tilde{\beta}_0 + \sum \tilde{\beta}_k \bar{x}_p}}{e^{\tilde{\beta}_0 + \sum \tilde{\beta}_k \bar{x}_p}},$$

where \bar{x}_p = average value of covariate p on the landscape. We used the RSF to estimate the relative use of the landscape by hunters for each 30m x 30m grid cell on the study area. We displayed this relative use as a color gradient with lighter colored areas representing greater use by hunters and darker colored areas representing less use.

Table 7. Variables included in models of distribution of hunters on the Sproul and Tuscarora study areas, Pennsylvania, 2005-2006.

Variable name	Description
ROAD	Distance from the nearest road (m)
SLOPE	Slope of the landscape (degrees)
OWNER	Land ownership (public, private)
ROAD ²	Squared distance from the nearest road (m ²)
SLOPE ²	Squared slope of the landscape (degrees ²)
ROAD*SLOPE	Interaction between distance and slope
ROAD*OWNER	Interaction between distance and land ownership
SLOPE*OWNER	Interaction between slope and land ownership

RESULTS

Capture Success and Causes of Mortality

During 2005-2007, we captured 203 female deer on the Tuscarora study area and 200 deer on the Sproul study area (Table 8).

Table 8. Number of deer captured on the Sproul and Tuscarora study areas, 2005-2007.

Year	Sproul Study Area		Tuscarora Study Area	
	Yearlings	Adults	Yearlings	Adults
2005	22	54	26	22
2006	19	35	25	28
2007	24	56	55	47
Total	55	145	106	97

Hunting was the most common source of mortality for collared deer but not all causes of mortality were determined (Table 9), although it is unlikely any mortalities of undetermined cause were the result of hunting. Most human-related mortalities other than hunting were vehicle collisions. Deer whose radio-collars failed were excluded because we assumed their fate was not related to the failure of the radio-collar.

Table 9. Number of mortalities, by cause of death, for all female white-tailed deer radio-collared, excluding capture-related mortalities, on two study areas in Pennsylvania, 2005-2007.

Cause of mortality	Sproul study area			Tuscarora study area		
	2005	2006	2007	2005	2006	2007
Hunting	4	5	13	9	14	17
Unknown	5	5	0	4	4	4
Unrecovered hunting ^a	2	0	1	2	3	1
Human related ^b	0	4	1	2	0	4
Natural causes	2	2	1	1	0	3
Poaching ^c	0	1	1	0	0	2

^a Deer not recovered by hunters but killed during the hunting season.

^b Excluding hunting, most mortalities represent vehicle collisions.

^c Poaching included illegal kills that occurred during the hunting season.

Annual Survival

The estimate of the annual survival rate for 2005 and 2006 incorporated hunting season, study site, land ownership, age of deer, and year as explanatory variables (Figure 4). On the Sproul study area, annual survival was greater on public land than private land, but was the opposite on the Tuscarora study area. Survival differed little between years or between age classes. Annual survival in 2007 was 82.2% (95% CI = 73.3–88.7%) on the Sproul study area and 71.3% (95% CI = 60.3–80.3%) on the Tuscarora study area.

Harvest Rate

For the Sproul study area, the estimates of harvest rate differed between the rifle season and other deer hunting seasons (archery and muzzleloader season) and differed between public and private land. Also, variables for year and age of deer were included in the model-averaged estimate of harvest rate. The final model-averaged harvest rates (Figure 5) from this model set indicated greater harvest rates among adults than juveniles, although marginally different, but much greater harvest rates on private land than on public land. The precision of harvest estimates on private land in 2005 had large confidence intervals because few radiocollared deer (9 of 55) were located on private land.

For the Tuscarora study area, estimates of harvest rate differed between the rifle season and other deer hunting seasons and differed between yearlings and adults. Also, variables for year and land ownership were included in the model-averaged harvest rate estimate. In contrast to the Sproul study area, harvest on the Tuscarora study area was greater among juveniles than adults, and greater on public land than private land.

In 2007, we found no differences between study areas or age classes but we did not investigate differences between public and private land. The harvest rate was estimated to be 18.3% (95% CI = 12.8–25.4%).

Spatial Distribution of Hunting Mortality

We found no landscape variables that were related to the spatial distribution of hunting mortality on the Tuscarora study area except that public land had greater harvest rates than private land (see *Harvest Rate* section of Results). For the Sproul study area, we found that the spatial distribution of hunting mortality was related to distance from road and slope (Figures 6-8). Deer hunting mortality decreased with increasing distance from road and increasing slope, regardless of land ownership. On public land, deer on 10° slopes experienced hunting mortality rates of 6.4% and 3.2% at distances of 0 m and 1,000 m from a road, respectively. Deer on private land on 10° slopes experienced mortality rates of 25.1% and 13.4% at distances of 0 m and 1,000 m from the nearest road, respectively. On public land, deer located 600 m from the nearest road experienced hunting mortality rates of 4.3% and 2.7% on slopes of 0° and 20°, respectively. On private land, deer that remained 600 m from a road experienced mortality rates of 17.5% and 11.3% on slopes of 0° and 20°, respectively.

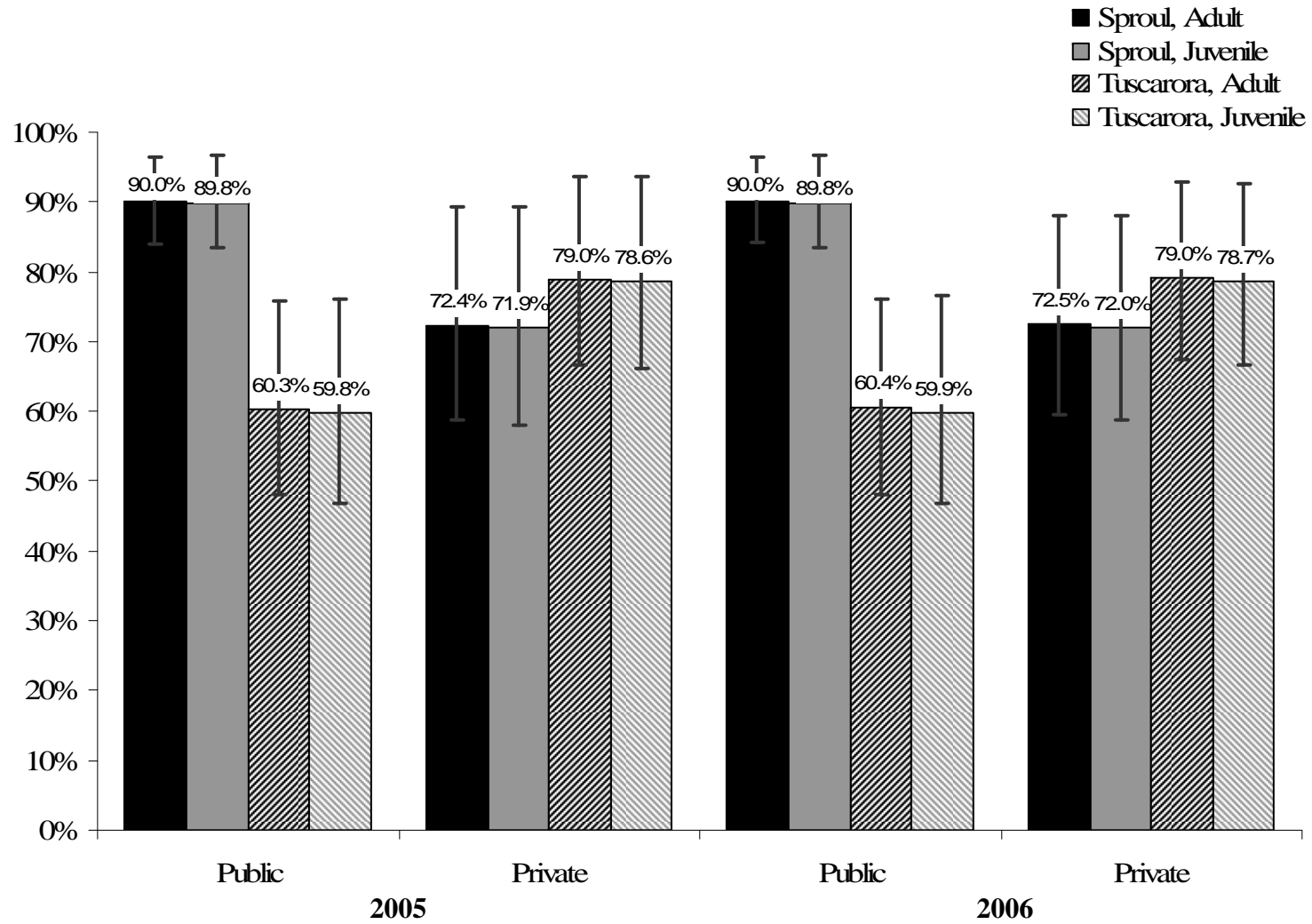


Figure 4. Annual survival of female white-tailed deer on the Sproul and Tuscarora study areas, Pennsylvania 2005-2006.

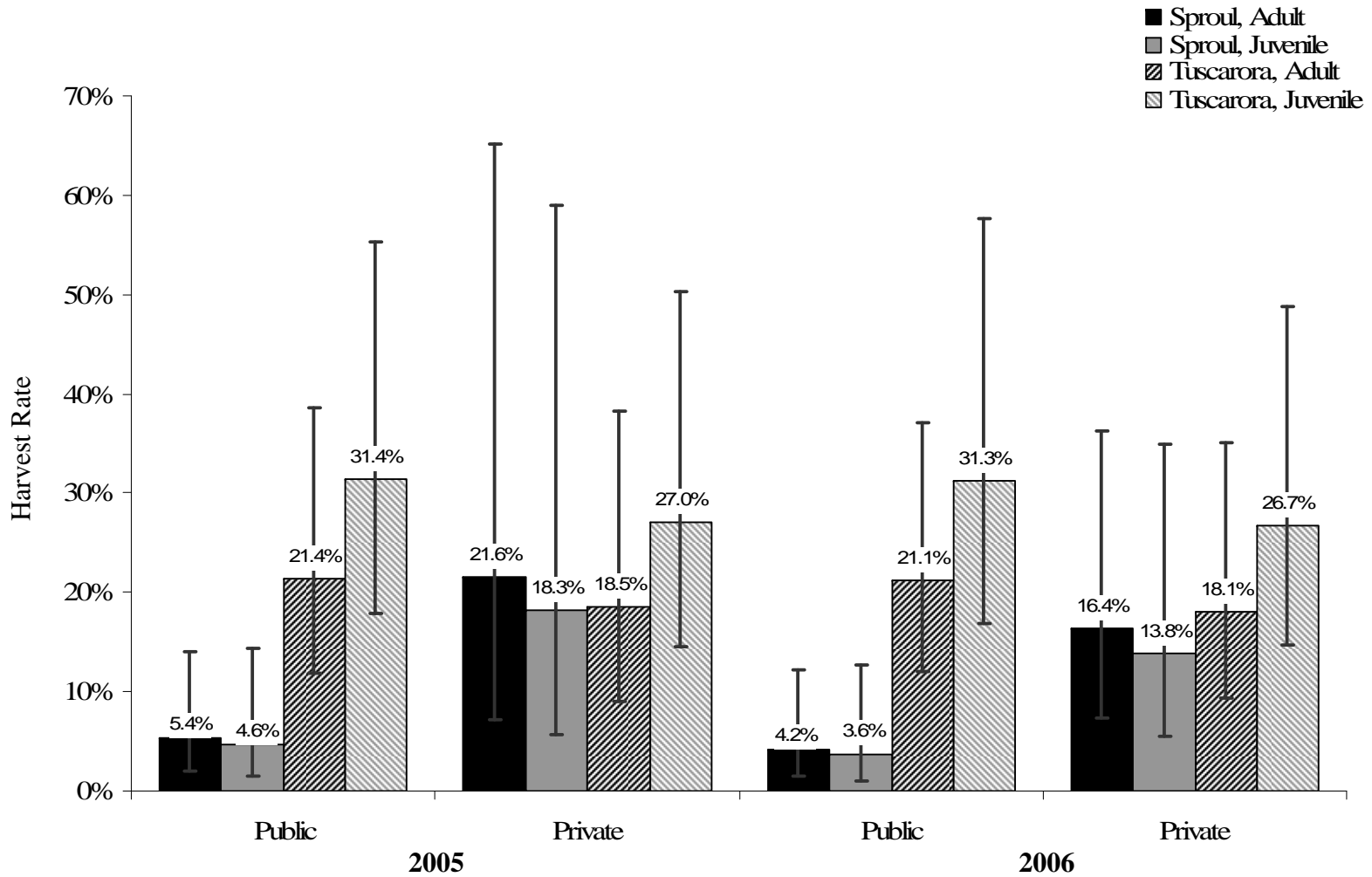


Figure 5. Harvest rates of female white-tailed deer on the Sproul and Tuscarora study areas, Pennsylvania, 2005-2006.

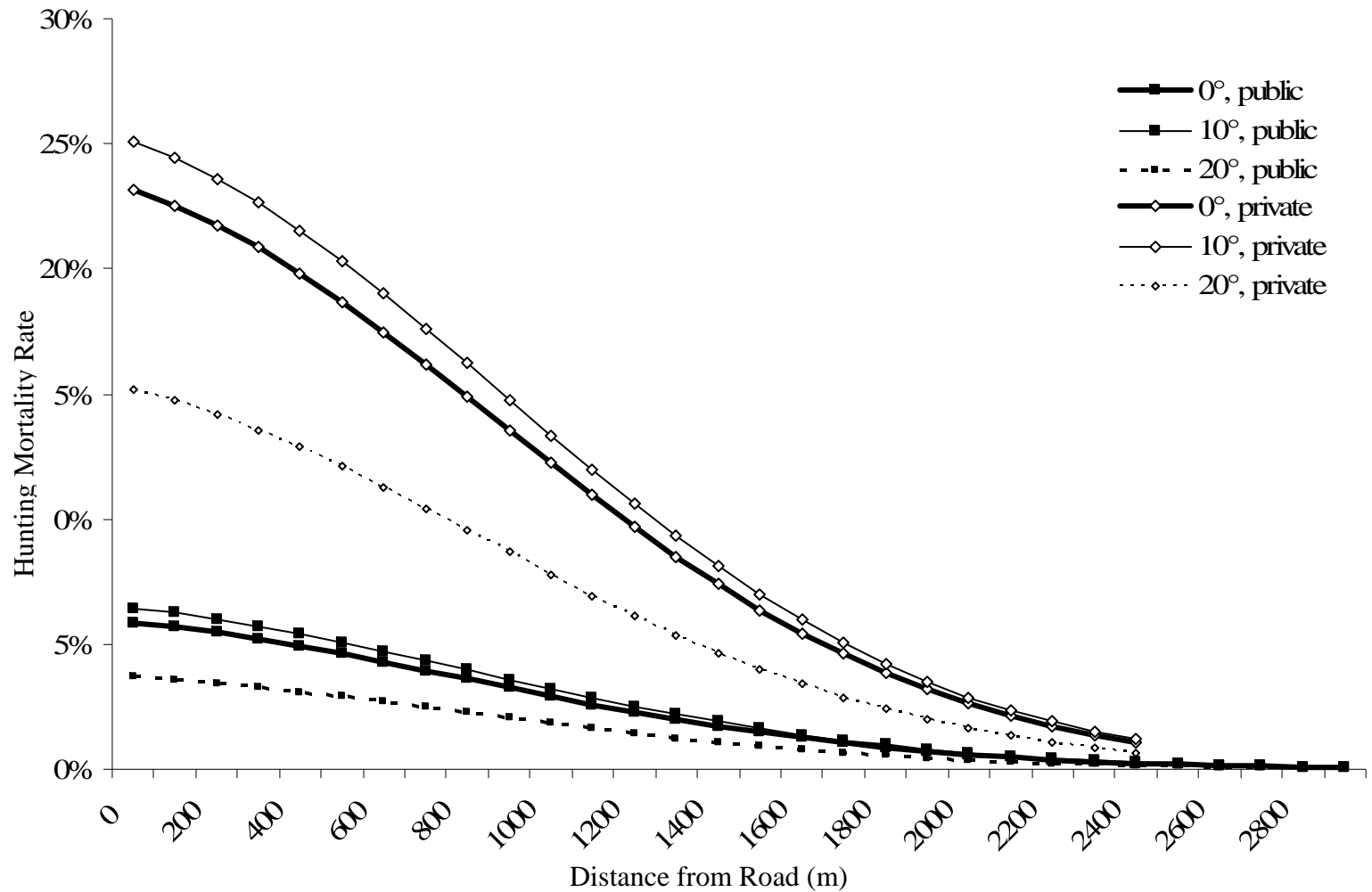


Figure 6. Hunting mortality rate of adult female white-tailed deer in relation to distance from the nearest road and three different slopes on the Sproul study area in north-central Pennsylvania, USA 2005-06.

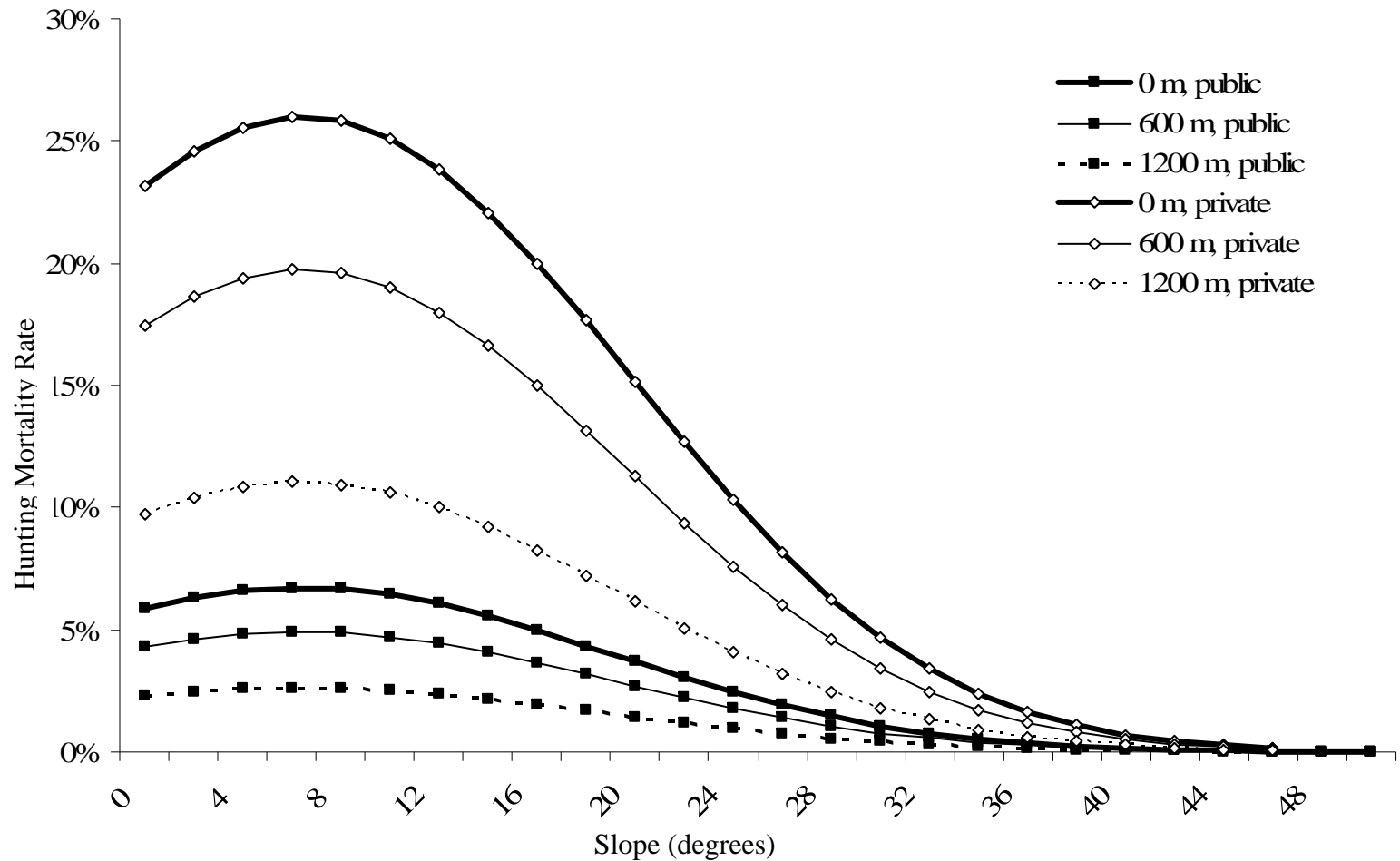


Figure 7. Hunting mortality rate of adult female white-tailed deer in relation to slope of the landscape and three distances from roads on the Sproul study area in north-central Pennsylvania, USA.

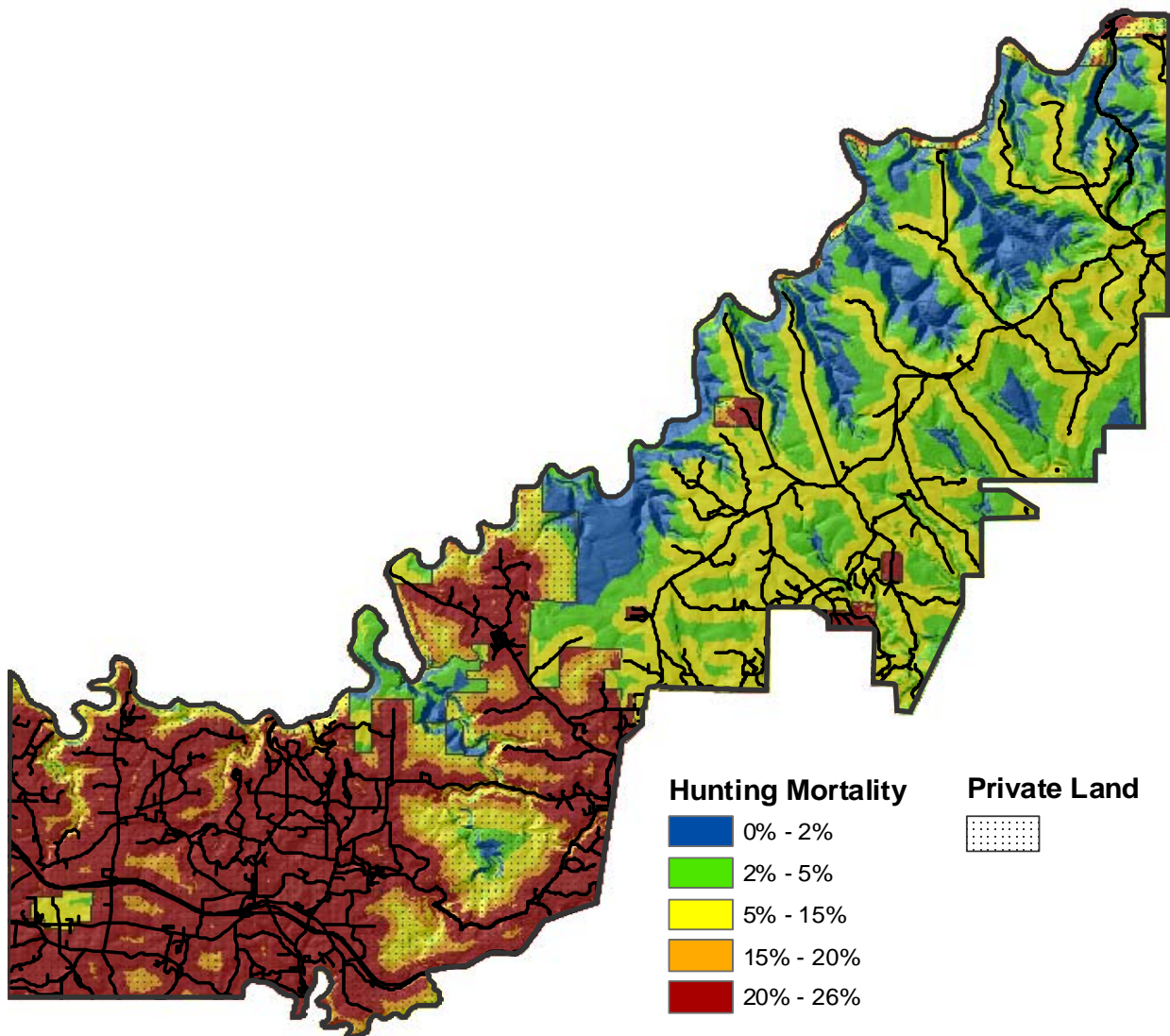


Figure 8. Map representing hunting mortality of female white-tailed deer on the Sproul study area in north-central Pennsylvania, USA 2005-06. Black lines represent roads.

Hunter Density

In 2005, adverse weather conditions prevented us from conducting surveys on either the first or second day of the rifle season, and we were unable to estimate hunter density for four flights on the Sproul study area because of equipment malfunction. Hunter density estimates were greatest during the first Wednesday on both study areas (Figure 9). Densities declined on following days until Saturday morning. Hunter densities the second week were lower and remained <0.1 hunters/km² until the last Saturday.

In 2006, favorable weather conditions allowed us to conduct hunter surveys during the first three days of the hunting season and on Saturdays. Hunter density on public land on the Sproul study area was greatest during opening morning (Monday) of rifle season, with 1.1 hunters/km² (Figure 10). Hunter densities were ≤ 0.4 hunters/km² every day from Wednesday afternoon until the end of hunting season. On private land on the Sproul study area hunter densities were similar to public lands (Figure 11). Monday and Tuesday morning experienced hunter densities of 1.0 and 1.1 hunters/km², respectively. Hunter densities during the second week of rifle season remained ≤ 0.4 hunters/km².

In contrast to the hunter density on the public land on the Sproul study area, hunter density on the public land on the Tuscarora study area increased during the first three hunts, from 0.9 to 1.1 to 1.2 hunters/km² during Monday morning, Monday afternoon, and Tuesday morning, respectively (Figure 10). Hunter densities were ≤ 0.3 hunters/km² during the second week. Hunter density on the private land on the Tuscarora study area decreased from 0.5 to 0.4 to 0.3 hunters/km² during Monday morning, Monday afternoon, and Tuesday morning, respectively (Figure 11). Hunter density was ≤ 0.3 hunters/km² during the remainder of the rifle season.

Spatial Distribution of Hunters—Sproul Study Area

Hunter distribution on the landscape differed on public and private lands. On public land, hunter use declined with increasing distance from the road and increasingly steeper slopes (Figures 12 and 13). In contrast, on private land, distance from road had little effect on hunter use, although they tended to use flatter slopes similar to hunters on public land (Figures 12 and 13).

Seventy-three percent of hunters on public land were located <600 meters from a road, compared to 60% of the study area being within that distance (Figure 14). Similarly, 70% of all hunters were located on slopes $<8^\circ$ on public land, which represented 57% of the study area (Figure 15). Hunters on private land were relatively uniformly distributed by distance from road (Figure 16), but 79% of hunters were on slopes $<8^\circ$ compared to 73% of the study area with slopes of $<8^\circ$ (Figure 17).

A chorograph of hunter distribution on the study area shows the spatial distribution of relative hunter use (Figure 18) on the Sproul study area.

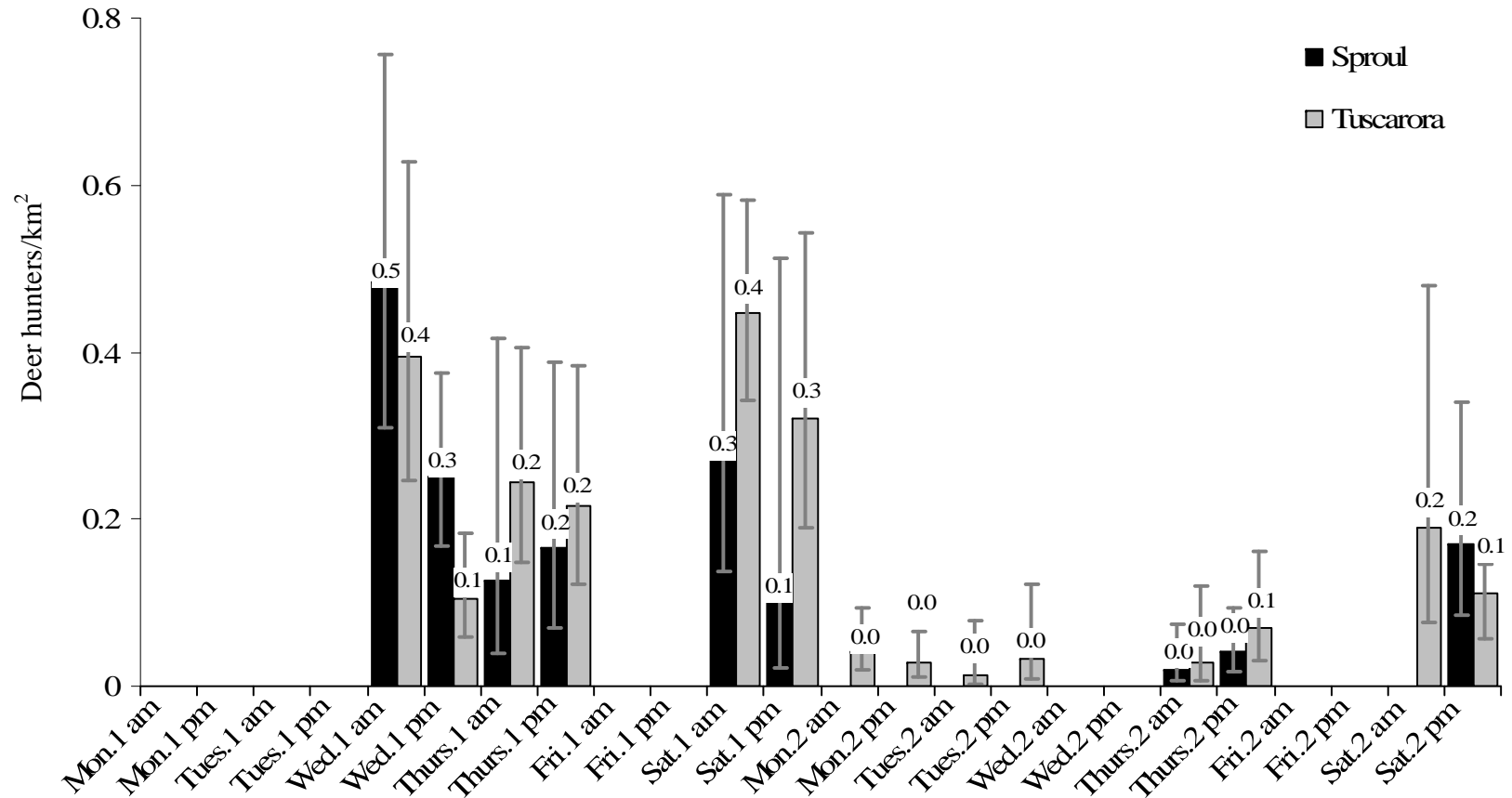


Figure 9. Hunter density on the Sproul and Tuscarora study areas, Pennsylvania, USA during the two-week regular deer rifle season, 28 November – 10 December 2005. Flight days with no data either were closed to hunting (Sunday) or experienced adverse weather conditions.

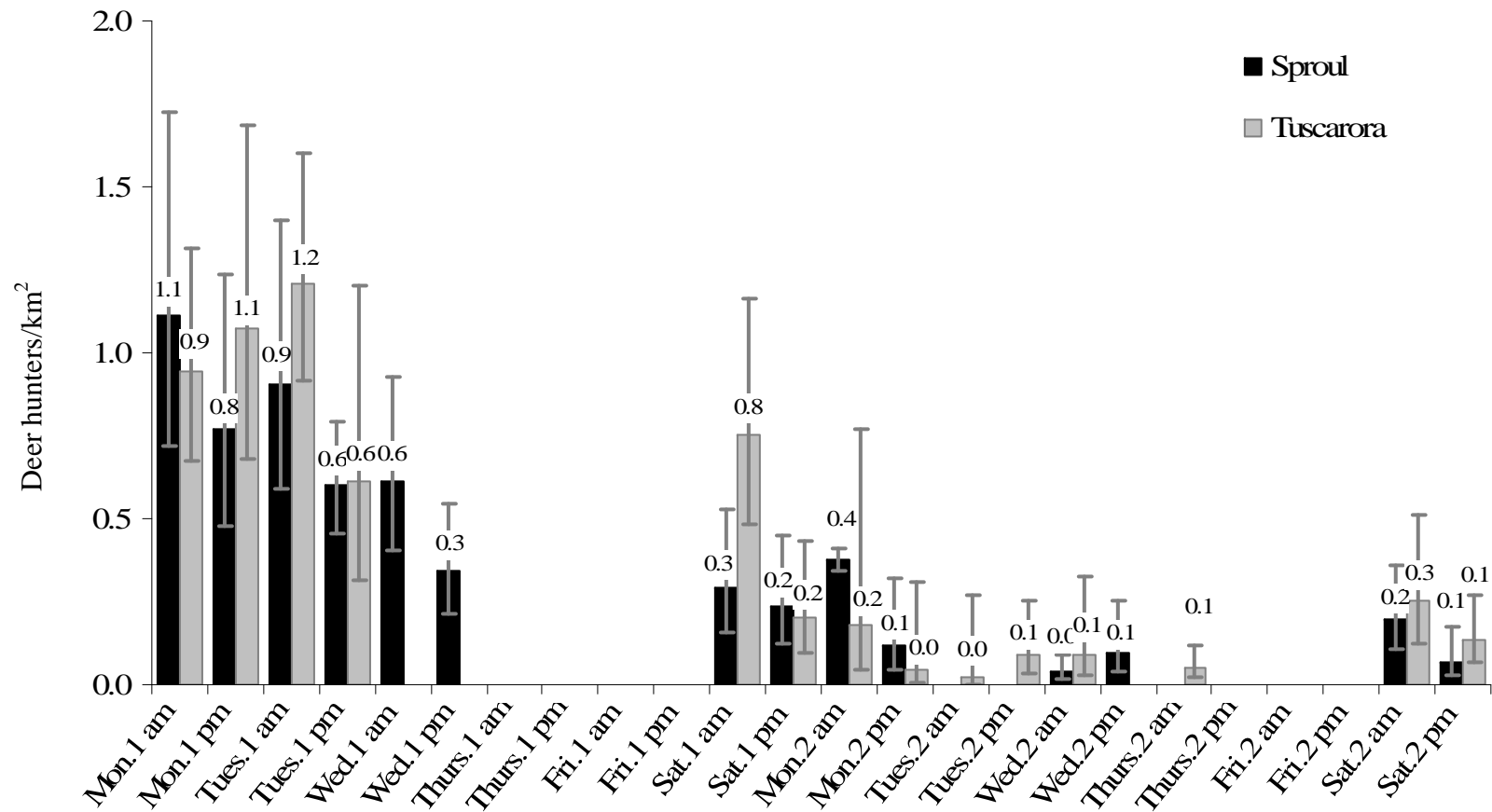


Figure 10. Density of deer hunters on the public land portions of the Sproul and Tuscarora study areas, Pennsylvania, USA during the two-week regular rifle season, 4-16 December 2006. Flight days with no data experienced adverse weather conditions. There is no Sunday deer hunting in Pennsylvania.

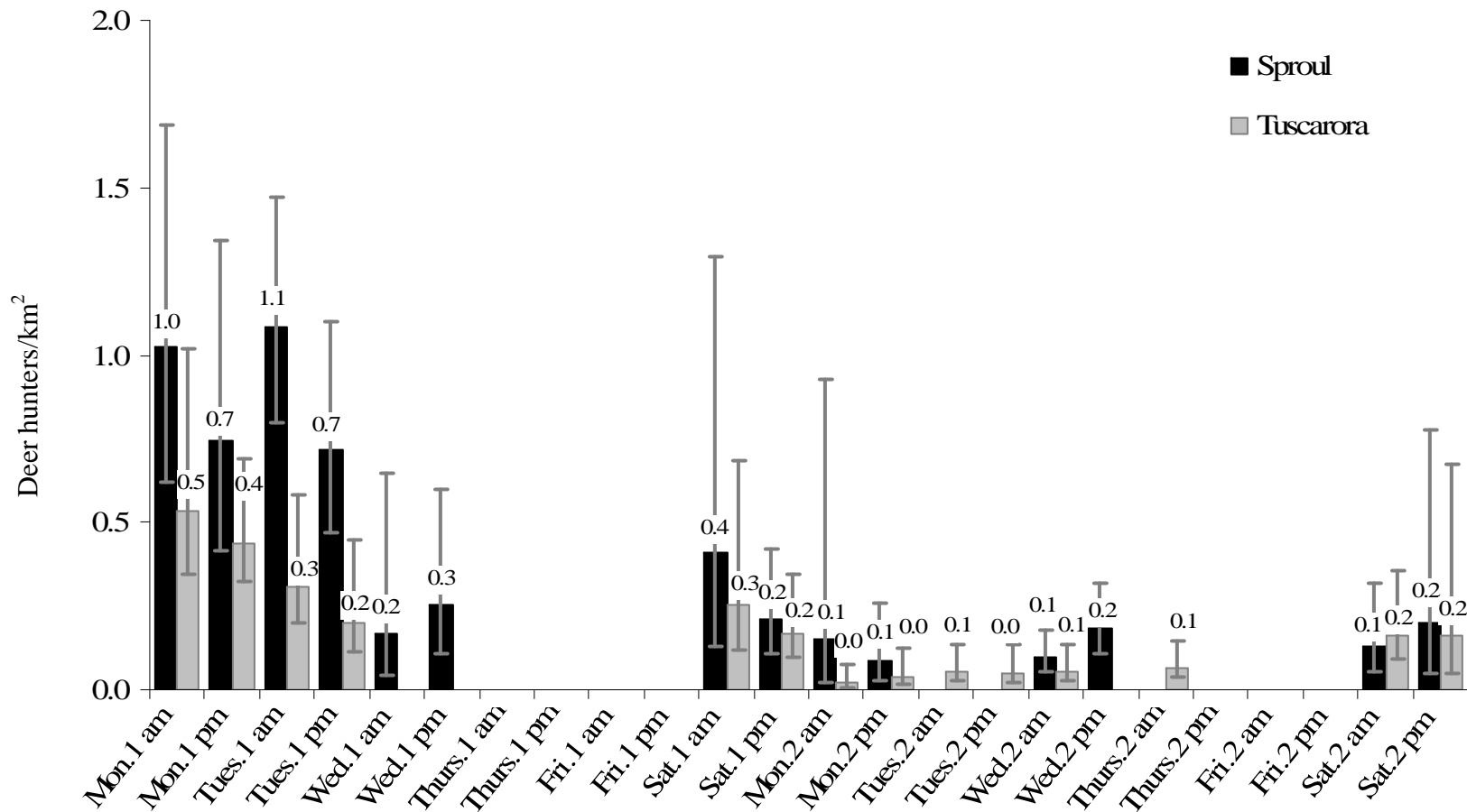


Figure 11. Density of deer hunters on the private land portions of the Sproul and Tuscarora study areas, Pennsylvania, USA during the two-week regular rifle season, 4-16 December 2006. Flight days with no data experienced adverse weather conditions. There is no Sunday deer hunting in Pennsylvania.

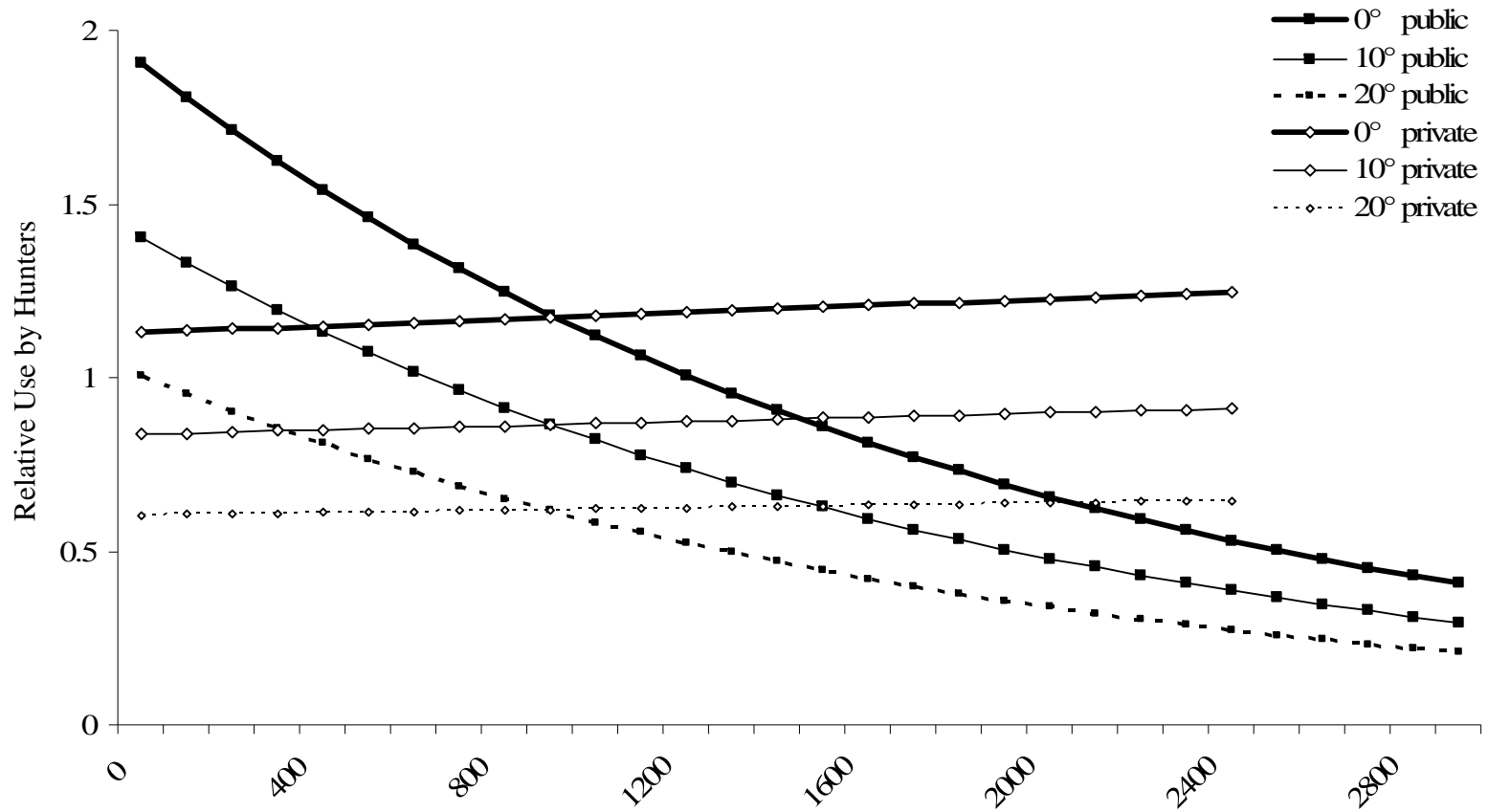


Figure 12. Hunter use as a function of distance from the nearest road for different slopes on Sproul study area, Pennsylvania, USA, 2006. A relative use value of 1 represents hunter use at the average distance and slope of the study area.

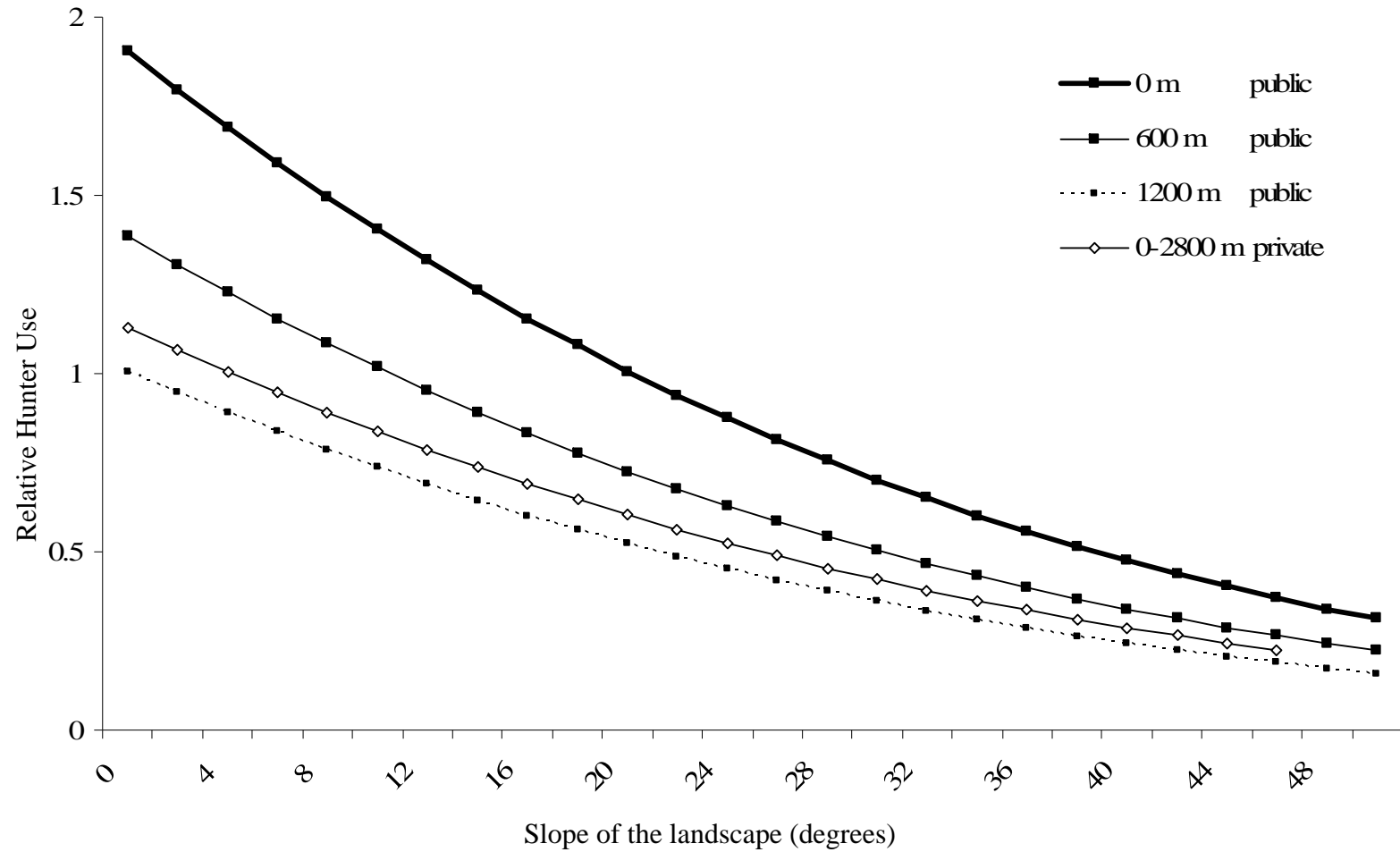


Figure 13. Hunter use as a function of slope for various distances from the nearest road on Sproul study area, Pennsylvania, USA, 2006. A relative use value of 1 represents hunter use at the average distance and slope of the study area.

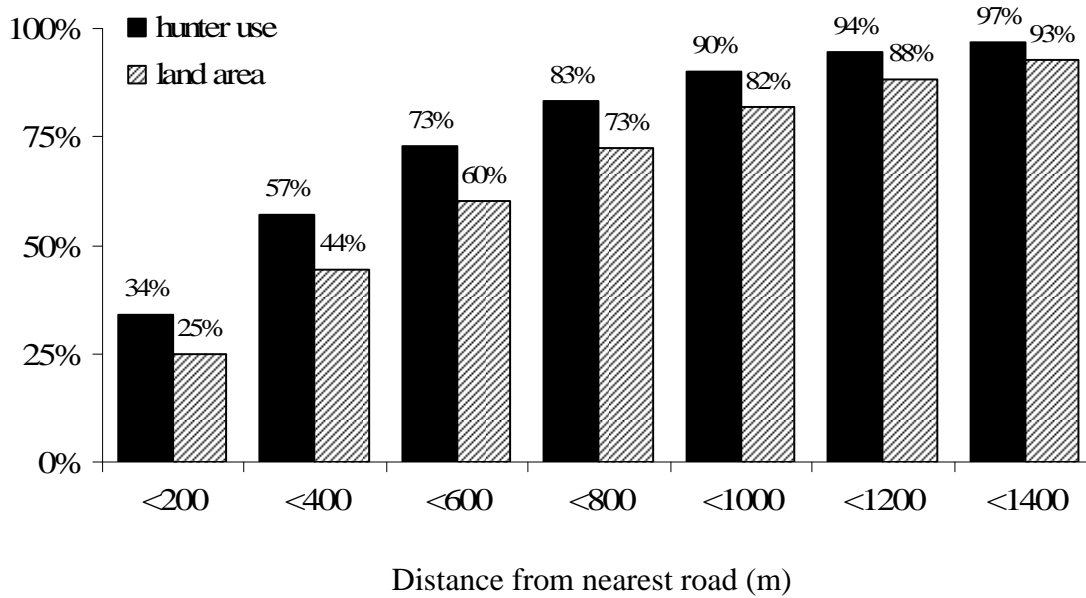


Figure 14. Cumulative distribution of hunters compared to available land area at various distance categories from roads open to the public on public land in the Sproul study area, Pennsylvania, 2006.

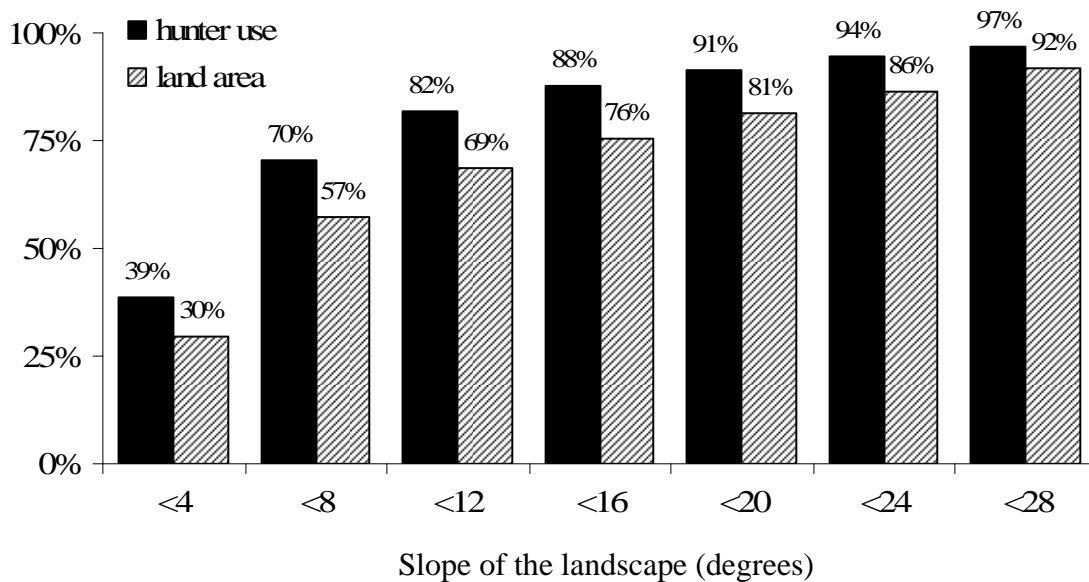


Figure 15. Cumulative distribution of hunters compared to available land of various slopes on public land in the Sproul study area, Pennsylvania, 2006.

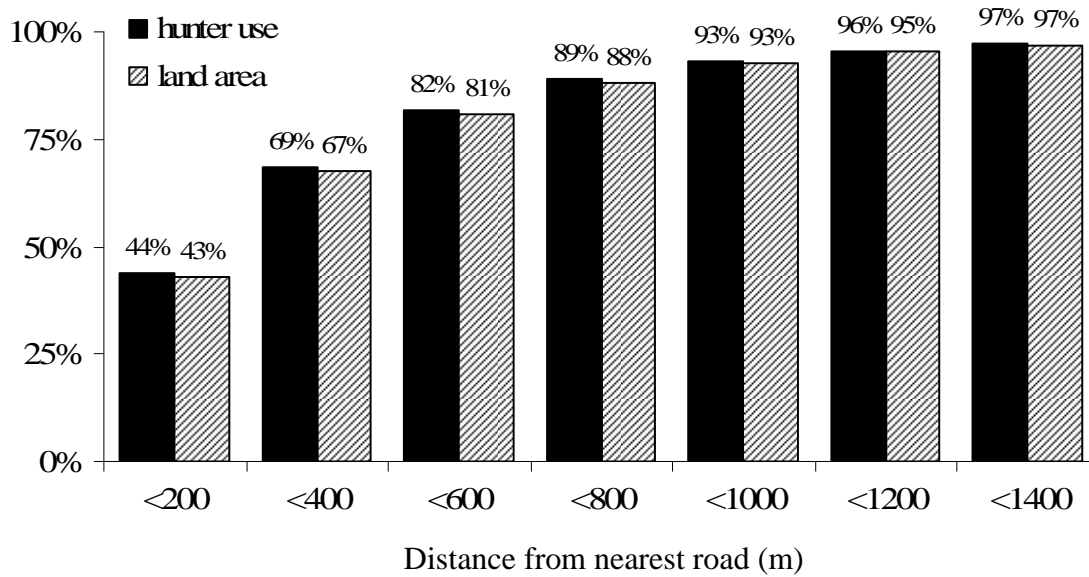


Figure 16. Cumulative distribution of hunters compared to available land area within various distances from the nearest public road on private land in the Sproul study area, Pennsylvania, 2006.

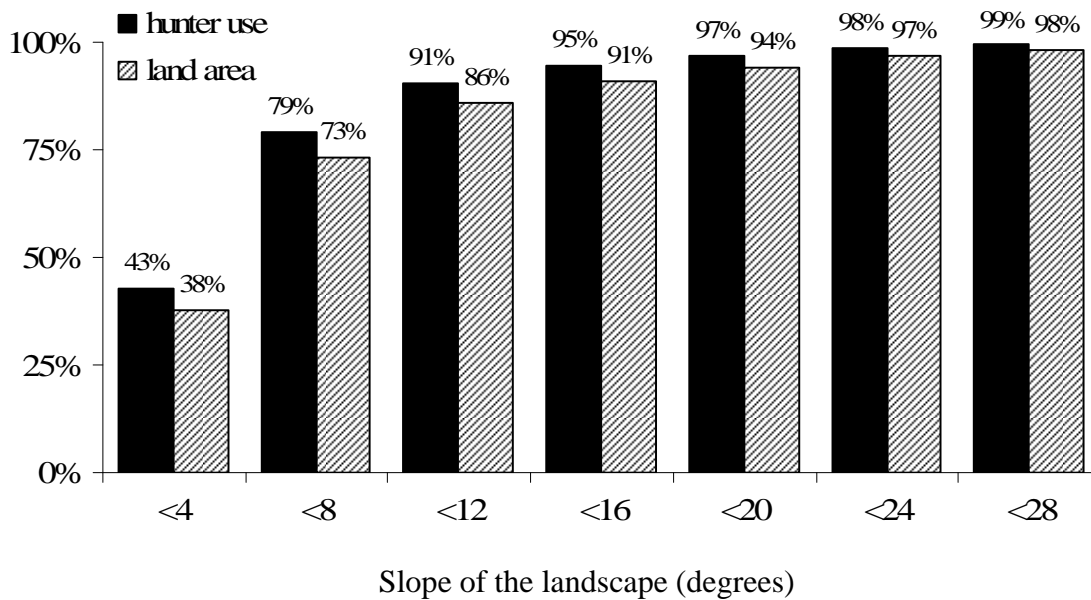


Figure 17. Hunter use compared to available land area within various slopes on private land in the Sproul study area, Pennsylvania, 2006.

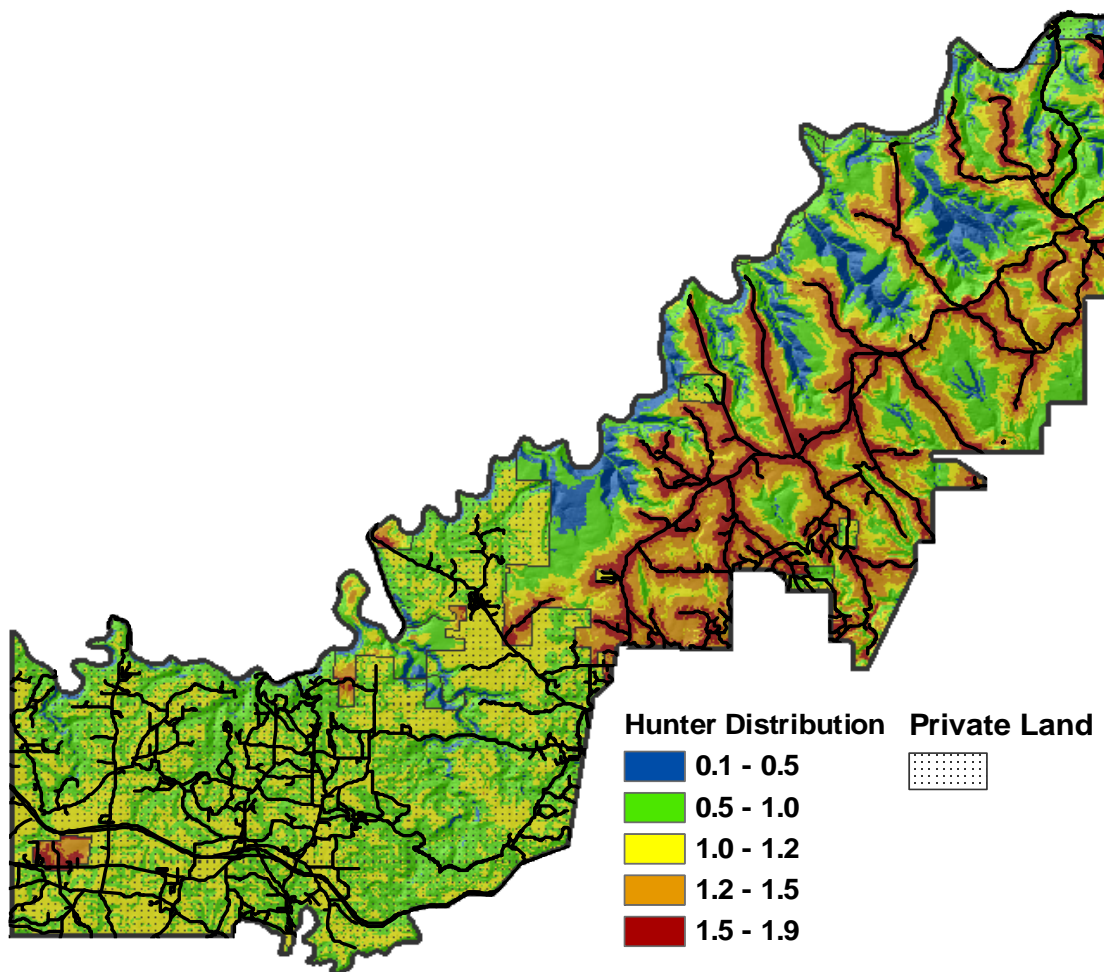


Figure 18. Hunter distribution (relative hunter use) on the Sproul study area in Pennsylvania, 2006. Average hunter use for the study area is represented by a value of 1. Gray stipples represent private ownership, and black lines represent roads. Hillshading is used to illustrate slope of the landscape.

Spatial Distribution of Hunters–Tuscarora Study Area

Overall, there were more hunters on public land than private land on the Tuscarora study area (Figures 19 and 20). On public land, hunters were found closer to roads and 79% of all public land hunters remained <600 m from a road, and 69% of the study area was within this distance from a road (Figure 21). Also, hunters tended to avoid steeper slopes but the effect was not as great as on the Sproul study area (Figures 20 and 22). Hunters on private land avoided locations both near and far from roads and slope had little effect on the distribution of hunters (Figures 19, 23, and 24).

The spatial distribution of hunters indicated the greatest hunter densities on public land near roads, and lowest hunter densities occurred on public and private land far from roads and private land very close to roads (Figure 25). Unlike the Sproul study area, there were few large, contiguous areas of low hunter density.

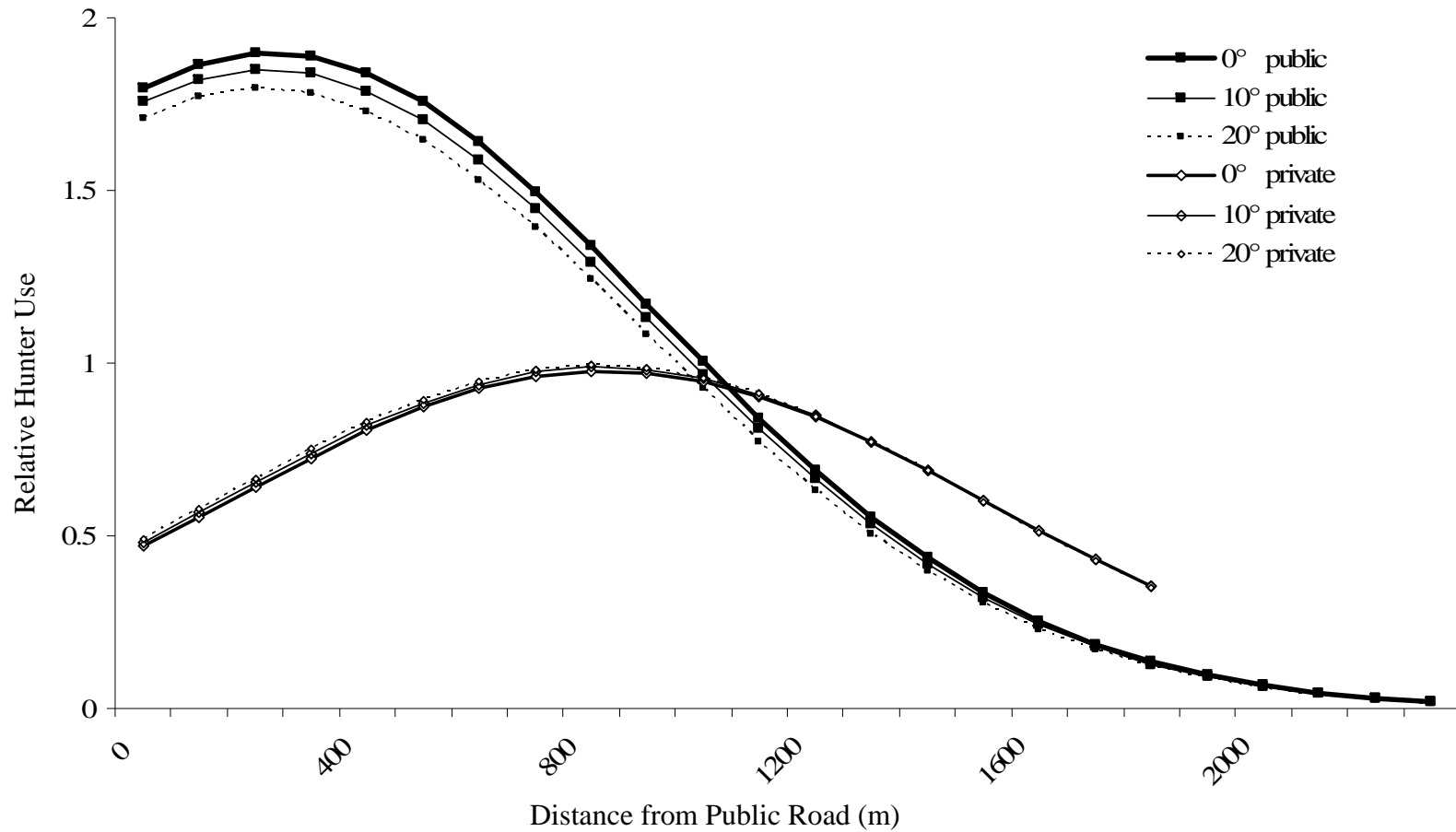


Figure 19. Relative hunter use as a function of distance from nearest public road on the Tuscarora study area, Pennsylvania, 2006. A relative hunter use value of 1 represents hunter use at the average distance and slope of the study area.

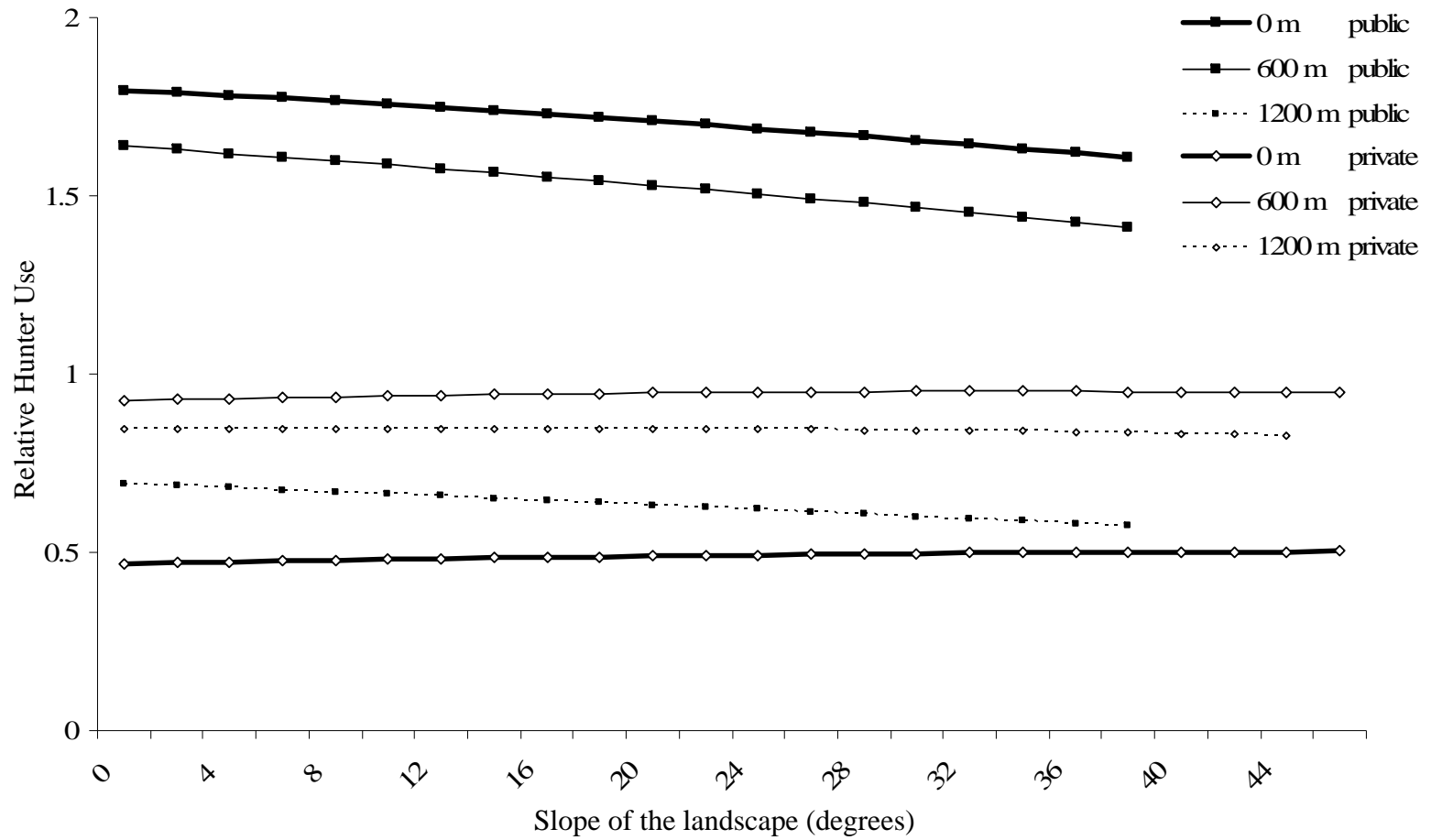


Figure 20. Relative hunter use as a function of slope for various distances from the nearest public road on the Tuscarora study area, Pennsylvania, 2006. A relative hunter use value of 1 represents hunter use at the average distance and slope of the study area.

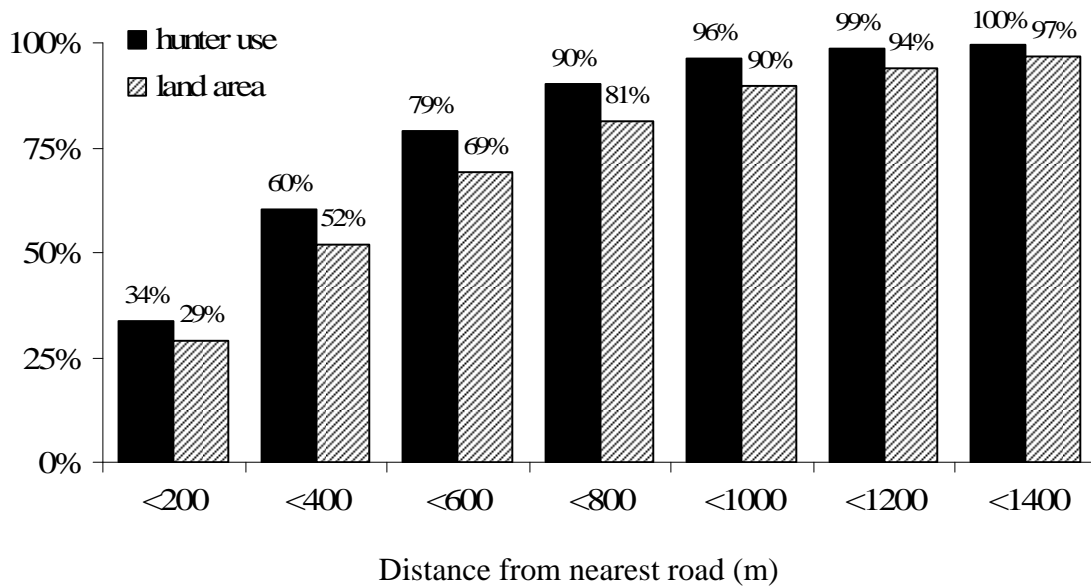


Figure 21. Cumulative distribution of hunters compared to available land area according to distance from the nearest road on public land in the Tuscarora study area, Pennsylvania, 2006.

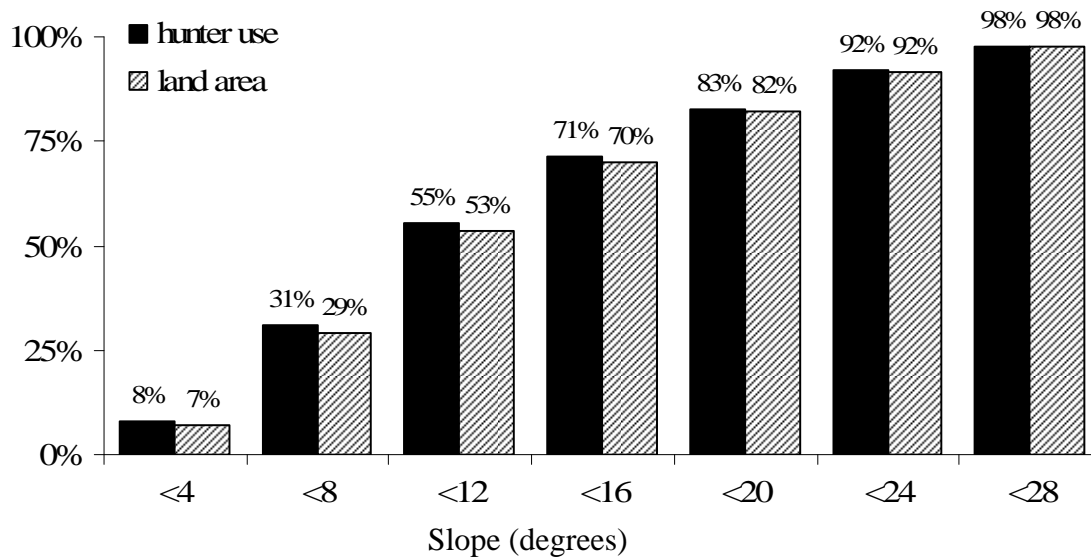


Figure 22. Cumulative distribution of hunters compared to available land according to slope of public land in the Tuscarora study area, Pennsylvania, 2006.

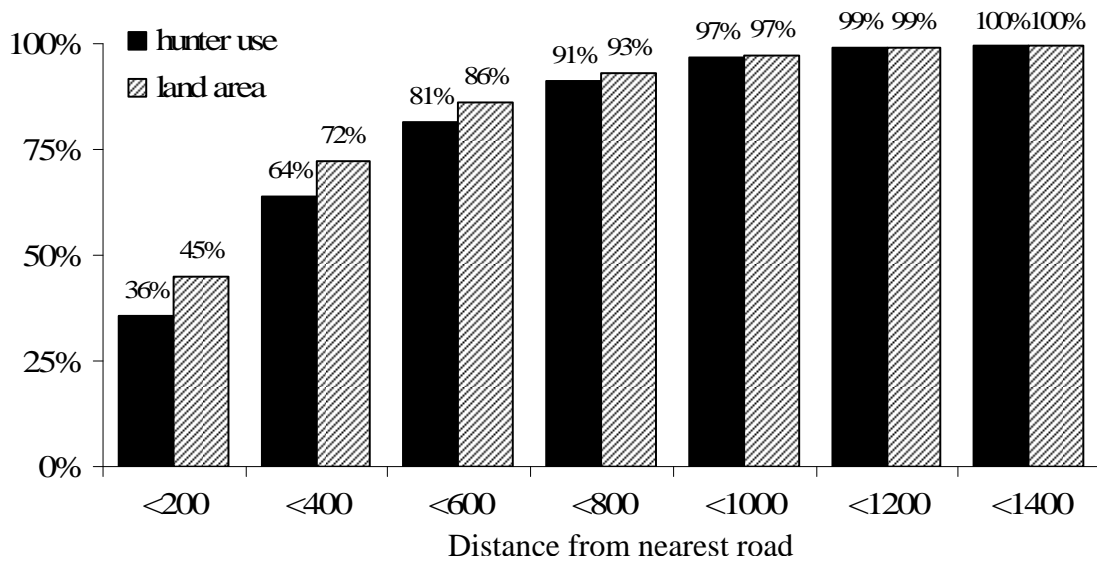


Figure 23. Cumulative distribution of hunters compared to available land area according to distance from the nearest public road on private land in the Tuscarora study area, Pennsylvania, 2006.

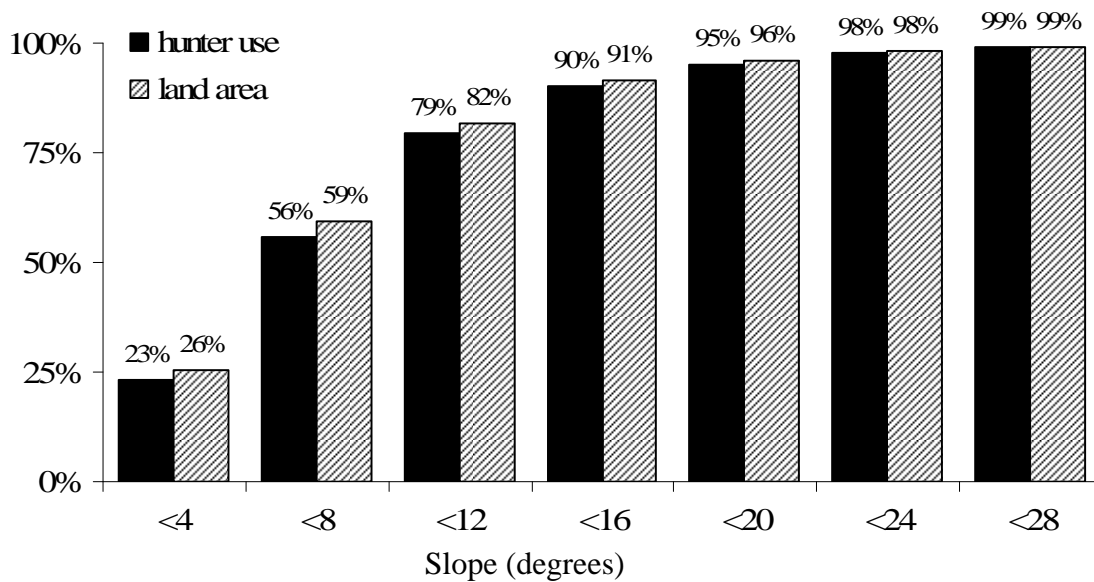


Figure 24. Cumulative distribution of hunters compared to available land area according to slope of private land in the Tuscarora study area, Pennsylvania, 2006.

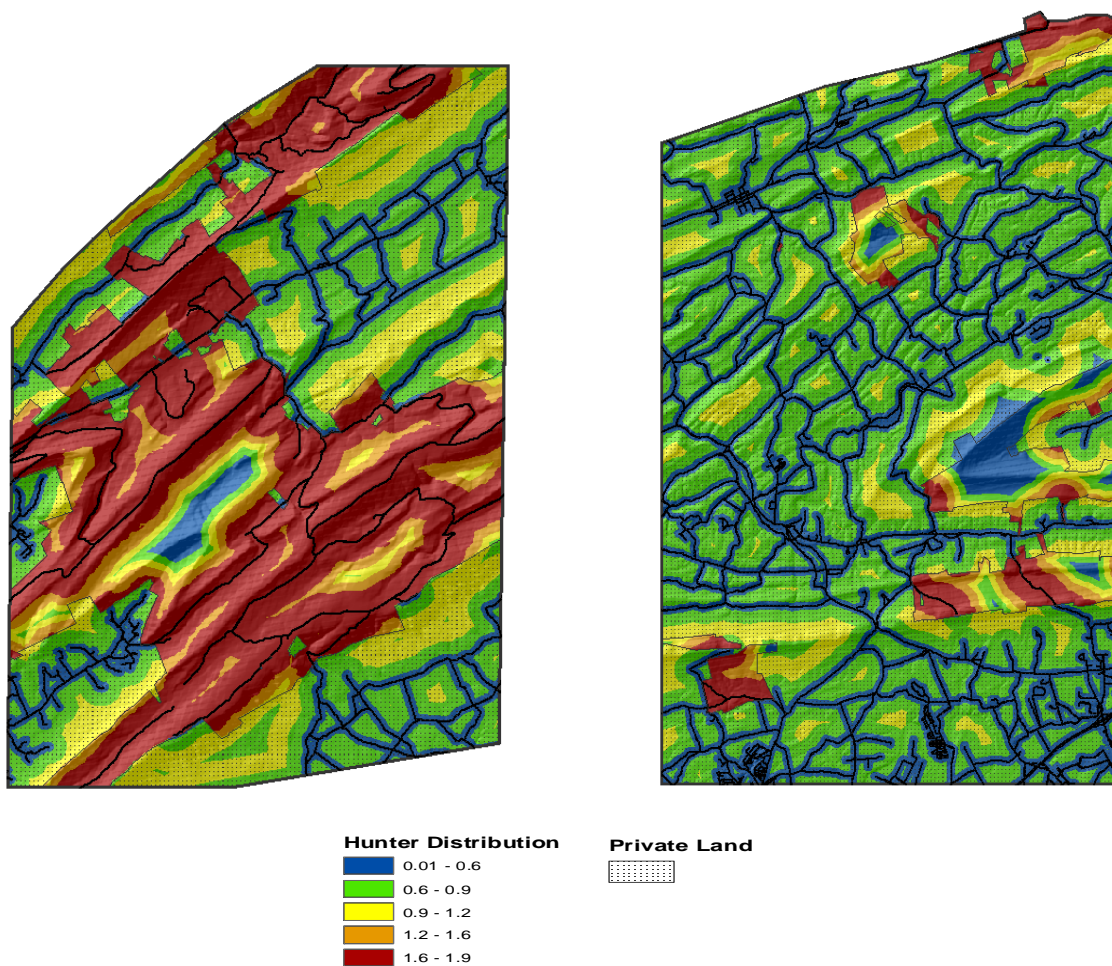


Figure 25. Relative hunter distribution on the Tuscarora study area, Pennsylvania, 2006. Average relative hunter use for the study area is represented by a value of 1. Gray stipples represent private ownership, and black lines represent roads. Hillshading is used to emphasize topographic relief.

DISCUSSION

We classified all deer that disappeared during the hunting season as legal harvests and, thus, may have overestimated the harvest rate. Also, we assumed that all radiocollars cut and abandoned were legally harvested if the mortality signal from the radio-collar indicated that the deer died during legal hunting hours. It is possible that some of these deer were killed illegally, resulting in an overestimate of the harvest rate and an underestimate of poaching. However, we know that some hunters refused to cooperate. For example, we detected a radiocollar signal leave the study area via a vehicle during an aerial survey and one radiocollar was surreptitiously placed on a tractor-trailer and reported from Philadelphia, Pennsylvania when the trailer cargo was unloaded. Consequently, we believe the few radiocollar signals that disappeared during the hunting season represent legally harvested deer.

Another issue that may have affected our estimates of survival and harvest rates was that a survey of hunters who participated in the DMAP program on the study areas indicated some hunters were reluctant to harvest radiocollared deer even if it were legal to do so (PGC, unpublished data). Given such findings, it is possible that radiocollared deer may have been harvested at a lower rate than other deer such that we underestimated harvest rates and overestimated annual survival. However, we note that an earlier study in Pennsylvania comparing harvest rates of male white-tailed deer fitted with ear-tag transmitters (that are difficult to see) and radiocollars exhibited no statistical difference in harvest rates (Long 2005, unpublished data). Furthermore, some of the oldest deer harvested in Pennsylvania are from WMU 2G, which suggests lower harvest rates, and is the same management unit where we observed low harvest rates on the Sproul study area (PGC, unpublished data).

In light of how hunter behavior may have affected our estimates of harvest and survival rates, these estimates should be interpreted with caution. However, the results from this study are still useful for examining relative differences in harvest and hunting mortality (e.g., between study areas or land ownership) and in examining relationships between hunting mortality and landscape characteristics.

Annual Survival Rates

Annual survival estimates from this study were similar to other published research with the exception of the public land portion of the Sproul study area, which experienced greater survival rates (Dusek 1989, Fuller 1990, Dusek et al. 1992, Van Deelen et al. 1997, Whitlaw et al. 1998). Annual survival rates of 90% on public land in the Sproul study area suggest that although this is a popular hunting location with liberal doe harvest regulations, hunting may have a limited effect on antlerless deer population dynamics. Non-hunted adult doe populations in northeastern Minnesota and New Brunswick experienced average annual survival rates of 79% and 85%, respectively (Nelson and Mech 1986, Whitlaw et al. 1998). Likewise, Van Deelen et al. (1997) estimated an annual

survival rate of 77% for adult females in northern Michigan under very strict harvest restrictions.

On both study areas, adults and juveniles experienced similar annual survival rates, indicating that once female deer survive to one year of age they have similar survival rates as older deer. Most published literature has found comparable survival rates for yearlings and adults (Nelson and Mech 1986, Dusek et al. 1992, Van Deelen et al. 1997). Also, hunting mortality is the greatest mortality factor, which is consistent with published literature (Dusek 1989, Fuller 1990, Dusek et al. 1992, Whitlaw et al. 1998).

Harvest Rate

The harvest rates on public lands in the Sproul study area were lower than those observed in published studies (Dusek 1989, Fuller 1990, Dusek et al. 1992, DelGiudice et al. 2002). Furthermore, in the same area, harvest rates were 4-5 time greater on private land. It is likely that the rugged terrain of this study area, and limited vehicle access on public land, precludes hunters from penetrating great distances from roads and harvesting deer. Our finding that female deer are most vulnerable close to roads and on flat slopes in the Sproul study area confirms the conjectures of Stedman et. al. (2004) and Diefenbach et al. (2005) when they reported more hunters used flat slopes and remained close to roads on the Sproul State Forest. Fuller (1988) found that hunter density in northern Minnesota also decreased with increasing distance from road. It is logical to assume that increased hunter density would result in increased hunting mortality, and our results support that assumed relationship. This is evident in Figures 8 and 18 that show areas of low hunter density have low harvest rates.

Also, the lower harvest rates on public land may be related to hunter attitudes. Hunters in the Sproul State Forest who hunt solely on public land are more reluctant to harvest female deer than hunters who hunt private land (Stedman et al. 2008). The relative difference in harvest rates between public and private portions of both study areas indicates that harvest rates vary significantly within each WMU. Furthermore, variability in harvest rates could vary greatly because of landscape characteristics (e.g., road access and topography).

The lack of any spatial variation in harvest rate on the Tuscarora study area is likely related to the distribution of roads, even though the ridges in this area have steep slopes similar to the Sproul study area. A harvested deer on steep slopes of the Tuscarora study area can be dragged downhill to a road whereas harvested deer on the Sproul study area have to be hauled uphill to the nearest road.

Hunter Density

The hunter density estimates for public land on the Sproul study area were similar to results from a previous study on the same study area conducted by Stedman et al. (2004) and Diefenbach et al. (2005). However, this study provides more information on hunting

effort during the first few days of the hunting season as well as adjoining private land. Moreover, it provides insight into hunter density and distribution in the Ridge and Valley province of Pennsylvania, which has different topography and road networks.

Hunter density on both study areas generally declined after the first two days, with increases on both Saturdays. This trend is consistent with published literature (Fuller 1988, Stedman et al. 2004, Diefenbach et al. 2005). We found evidence of a shift in hunting density between the first and second mornings (Monday and Tuesday) of the regular rifle season. In the Sproul study area, hunter density decreased on public land and increased on private land whereas hunter density on the Tuscarora study area increased on public land and decreased on private land. This shift in hunting pressure may be related to changes in harvest success rates of hunters between public and private lands, or hunter behavior with respect to when and where hunters choose to hunt, or differences between hunters who hunt public versus private land. More research is needed to understand the changes we observed in hunter density.

Spatial Distribution of Deer Harvest and Hunters

The distribution of hunting mortality for public land on the Sproul study area indicated large areas of land that experienced hunting mortality rates of <2% (Figure 8) and hunter distribution indicated low hunter density in these same areas (Figure 18). These areas of few hunters and low hunting mortality rates may serve as *de facto* refugia for deer. Research suggests that deer populations with access to refugia are likely to maintain or increase in number even if they are being harvested at high rates in areas adjacent to the refugia (Joshi and Gadgil 1991, Brown et al. 2000, Novaro et al. 2000, Siren et al. 2004). Thus, extended hunting seasons and increased number of DMAP permits could have minimal effect on deer population dynamics. If so the only way to minimize the effect of refugia would be to increase hunter access to locations far from public roads and on steep slopes.

The distribution of hunters on public land on the Tuscarora study area indicated relatively uniform distribution with only a few, small areas with few hunters. Furthermore, overall hunter density was greater on public lands. Consequently, we found no spatial variation in hunting mortality rates of deer, except that harvest rates were greater on public land than private land.

On private lands on both study areas we found a relatively uniform distribution of hunters. This is likely because use of vehicles is not regulated except by the landowner. Consequently, except for very steep slopes, hunters had access to most of the landscape. The fewer hunters close to roads on private land on the Tuscarora study area is likely because these areas were not forested and unlikely to be good hunting areas for deer. As a result, on private lands we found no evidence for deer refugia. This would suggest that on private land, extended days of hunting and a greater number of licenses to harvest antlerless deer would likely increase the harvest rate on female deer.

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