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School of Forest Resources

HUNTER DISTRIBUTION AND HARVEST OF FEMALE WHITE-TAILED DEER IN PENNSYLVANIA

A Thesis in

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by

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ABSTRACT

In 2001 and 2003, the Pennsylvania Game Commission increased opportunities for hunters to harvest antlerless white-tailed deer (*Odocoileus virginianus*) as part of an effort to change the densities and age-sex structure of deer populations in most wildlife management units. However, areas that experience low levels of hunting effort and deer harvest may serve as *de facto* refugia where such regulation changes could have little influence on deer densities. Knowledge of spatial variation in deer harvest and hunter distribution may help managers direct hunting effort to more effectively regulate deer densities.

I captured, collared, and monitored 231 antlerless white-tailed deer from 2005 to 2006 surrounding the Sproul State Forest in north-central Pennsylvania and the Tuscarora State Forest in south-central Pennsylvania. I monitored deer on a weekly basis to estimate annual survival and harvest rates and to model spatial distribution of hunting mortality. I conducted aerial surveys of hunters during the 12-day rifle hunting seasons in 2005 and 2006 on these same areas to estimate hunter density and to model hunter distribution. I compared the distributions of hunters and hunting mortality to identify spatial variation in hunting efficiency. Lastly, I used these models to predict the effect of an expanded road network on hunting mortality and refugia.

Point estimates indicated that on the Sproul study area, annual survival was greater on public land (89.9%, 95% CI = 84.0-96.1%) than private land (75.5%, 95% CI = 66.7-85.6%), but was the opposite on the Tuscarora study area (60.9%, 95% CI = 49.4-75.2% on public land and 75.5%, 95% CI = 66.7-85.6% on private land). Point estimates indicated harvest rates on the Sproul study area were almost four times greater on private land (16.7%, 95% CI = 8.4-33.2%) than on public land (4.4%, 95% CI = 1.8-10.8%). On the Tuscarora study area, harvest rate did not vary between public and private land, but point estimates indicate subadults were harvested at almost twice the rate (30.3%, 95% CI = 19.0-48.1%) as adults (16.4%, 95% CI = 9.4-28.6%). The high survival and low harvest rates on public lands in the Sproul study area suggest that hunting may have a limited effect on deer population dynamics.

Hunter density on both study areas was greatest early in the hunting season. On the Sproul study area, a maximum hunter density of 1.1 hunters/km^2 was observed on both public and private land during opening day of the rifle season. Hunter densities on public portions of Tuscarora study area ranged from 0.9-1.2 hunters/km^2 over the first two days of the rifle season. Hunter density on Tuscarora's private lands was lower, with a maximum hunter density of 0.5 hunters/km^2 observed on opening morning.

On both the Sproul and Tuscarora study areas, hunter use generally declined with increasing distance from the nearest public road and with increasing slope of the landscape. On the Sproul study area, 73% of hunters on public land were located <600 m from a road, compared to 60% of the area being within that distance and 70% of hunters used slopes <8°, which represented 57% of the area. Hunters on private lands on the Sproul study area were uniformly distributed by distance from road, but 79% of hunters were on slopes <8°, which represented 73% of the area. On the Tuscarora study area, 79% of all public land hunters remained <600 m from a road, compared to 69% of the area being within that distance, and hunters tended to avoid steeper slopes, although the effect was not as great as on the Sproul study area. Hunters on private land in the

Tuscarora study area avoided locations both near and far from roads and slope had little relation to the distribution of hunters.

I found no spatial variation in deer hunting mortality rate on the Tuscarora study area. On the Sproul study area, hunting mortality was highest close to roads, likely because hunter use was concentrated in those areas. On public land, 74% of all hunting mortality occurred <500 m from a road, although only 53% of the area was within that distance. On private land, 87% of all hunting mortality occurred <500 m from a road, compared to 74% of the area being within that distance category. Slope of the landscape, however, had little influence on deer hunting mortality.

Hunting efficiency was not uniform across the landscape, indicating deer were more vulnerable to harvest in some areas, regardless of hunting pressure. Hunters were most efficient 500–1,000 m from a road and on moderate slopes between 10 and 20 degrees. Hunting efficiency also increased with increasing hunter use, except in areas of greatest use.

The Sproul study area contained >4,000 ha of *de facto* refugia that experienced hunting mortality rates of <2%, and increased opportunities for hunters to harvest antlerless deer may have little effect on deer densities in these areas. Increasing hunter access to refugia may be an effective way to control local deer populations and expanding the public road network to include all gated and unimproved roads could potentially decrease the amount of refugia by 67%.

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Chapter 1

Introduction

White-tailed deer status, management, and socio-economics in Pennsylvania

The white-tailed deer (*Odocoileus virginianus*) in North America has expanded its range over the last 100 years because of changes in land use 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/km^2 in pre-settlement times to present-day estimates averaging >11/km^2 and as high as 31/km^2 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) and by the the late 20th century, densities were approximately twice that of established goals (Diefenbach and Palmer 1997, Diefenbach et al. 1997). In 2001 and 2003, the Pennsylvania Game Commission (PGC) changed deer hunting regulations to create changes in densities and age-sex structure of 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), increased the number of licenses to harvest antlerless deer, and instituted a Deer Management Assistance Program (DMAP) to provide landowners permits to harvest antlerless deer on their property.

An estimated 932,000 deer hunters in Pennsylvania added approximately $476 million to the Commonwealth's economy through hunting-related expenditures in 2001 (U.S. Department of the Interior and U.S. Department of Commerce 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 12 Pennsylvanians hunted deer in 2002 (U.S. Department of the Interior and U.S. Department of Commerce 2003, U.S. Census Bureau 2004). Many Pennsylvania deer hunters traveled to a lodge or cabin with extended groups of friends or family, which demonstrates the tradition and social significance of deer hunting to Pennsylvanians (Zinn 2003).

Harvest and hunting mortality

The harvest rate is the proportion of animals in a population that are legally killed and recovered by human 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). Harvest reports can be used to estimate total harvest but do not estimate harvest rates. 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 from this sample can provide estimates of the harvest rate (Heisey and Fuller 1985, Pollock et al. 1989). The hunting mortality rate is the proportion of deer that are legally harvested, killed illegally during the hunting season, and fatally shot but not recovered (wounding loss). Hunting mortality represents the effect of hunting on a population.

Researches have found hunting is the primary cause of deer mortality in areas with legal hunting seasons (Dusek 1989, DelGiudice 2004). Reported hunting-related annual mortality rates of female white-tailed deer range from 10% in New Brunswick (Whitlaw et al. 1998) to 22% in Montana (Dusek et al. 1992). Hunting mortality rates as low as 4% have been reported from locations with restrictive harvests of females (Van Deelen et al. 1997). 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 range from 66% in New Brunswick (Whitlaw et al. 1998) to 78% in Montana (Dusek 1989).

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

The PGC increased harvest opportunities for antlerless deer by providing additional permits to landowners through DMAP in 2003 and by increasing the length of the antlerless rifle season in 2001. The Sproul and Tuscarora State Forests were enrolled in DMAP in 2005 and 2006, therefore harvest estimates of these study areas may provide insight to the effectiveness of this program. These harvest data also would help natural resource managers and hunters understand the effect of hunting on Pennsylvania's deer herd.

Hunter density and distribution

Few studies have estimated spatial variation in hunters. Broseth and Pederson (2000) modeled the distribution of hunters of willow ptarmigan (*Lagopus lagopus*) as a function of distance from a base camp and Fuller (1990) found deer hunter density decreased with increasing distance to road. Other research on hunter density and distribution is of limited relevance to this project. Millspaugh et al. (2000) modeled 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.

Existing literature on deer 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 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/km^2. However, adverse weather conditions restricted the time period of data collection to 1000–1200 hours on opening morning in 2001, and postponed research until the second day of rifle season in 2002. Hunter densities likely are greatest during 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/km^2 on opening morning in northern Minnesota.

Diefenbach et al. (2005) concluded hunters were not distributed evenly across the landscape, but rather selected flat areas close to roads. Only 56% of the area was located within 0.5 km of a drivable road yet 87% of hunters were found within that distance to a road. 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 hunters in northern Minnesota, USA were located within 0.8 km of roads, which represented 50% of the study area.

Diefenbach et al. (2005) and Stedman et al. (2004) provided a foundation of 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. 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.

Spatial distribution of hunting mortality

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 access to increase the harvest rate of the overall population. In such areas, activities such as opening and maintaining roads or allowing all-terrain vehicle access may be more effective than increasing license allocations or season length.

Deer vulnerability to harvest (hunting efficiency) also may vary across the landscape, regardless of hunting pressure. A greater understanding of spatial variation in hunting efficiency could help land managers to increase hunter access to areas not used by hunters.

To my knowledge, only one study has examined the distribution of deer hunters and deer hunting mortality. Fuller (1988) concluded deer hunter density and hunting mortality rate decreased with each of three increasing distance to road categories. Broseth and Pedersen (2000) concluded harvest of willow ptarmigan was predicted by hunting pressure modeled as a function of distance from a base camp. Other studies have compared harvest rates of white-tailed deer on study areas with variable habitat conditions such as forage type and quantity, dominant tree species, hectares of clearcuts, kilometers of roads, and number of hunters (Kammemeyer and Moser 1990, Dusek et al. 1992). A statistical model of the spatial distribution of antlerless deer hunting mortality 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 and 2006. Because hunter participation is historically greatest during the regular rifle season (28 November–10 December 2005 and 4–16 December 2006), I limited my research on hunter density and distribution to these dates.

Research objectives

I captured female white-tailed deer on two study areas in Pennsylvania, USA and monitored their movements and fate. I used this information to quantify landscape features associated with the fate of each deer during the hunting season. Also, I conducted aerial surveys and recorded the locations of hunters during the 12-day rifle season to estimate hunter density and distribution across the study areas. Other studies have examined harvest rates of white-tailed deer (Fuller 1990, Dusek et al. 1992, Van Deelen et al. 1997, Whitlaw et al. 1998) and Diefenbach et al. (2005) modeled hunter distribution on one of my study areas. However, to my knowledge, no one has linked the distribution of hunters and how that may be related to the distribution of deer harvest.

Therefore, the first objective of my research was to estimate annual survival and harvest rates of female white-tailed deer and model the spatial distribution of hunting mortality on each study area. The second objective was to estimate hunter density and model the spatial distribution of hunters. The third objective was to model the spatial relationship between deer hunting mortality and hunter distribution to identify areas of low hunting mortality (i.e., refugia) and use these models to investigate the effect of management actions to modify hunter access to increase deer harvest mortality.

Chapter 2

Study Areas

I selected two study areas encompassing large tracts of public land, primarily forested, managed by the Bureau of Forestry, Department of Conservation and Natural Resources, and enrolled in the PGC's DMAP. The study areas were located on and around the Sproul and Tuscarora state forests, in north-central and south-central Pennsylvania, respectively (Figure **2-1**). Research was limited to public lands on both areas in 2005, but expanded to private lands in 2006. These study areas were located in the two largest physiographic provinces in Pennsylvania that account for >87% of the state's land area.

Sproul study area

The Sproul study area was located primarily 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 49% public land. The forest is in the transition zone of the mixed-oak hardwoods and northern hardwoods and is dominated by red oak (*Quercus rubra*), white oak (*Quercus alba*) sugar maple (*Acer saccharum*), black birch (*Betula lenta*), American beech (*Fagus grandifolia*), yellow poplar (*Liriodendron tulipifera*), white pine (*Pinus strobus*), scarlet oak (*Quercus coccinea*), chestnut oak (*Quercus prinus*), and black cherry

(*Prunus serotina;* Cuff et al. 1989). Annual snowfall at the Renovo, Pennsylvania weather station averaged 28.1 inches from 1971-2000 (National Oceanic and Atmospheric Administration 2002). Deer productivity was 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 **2-2)**. 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. Plateaus were dissected by steep drainages to the West Branch of the Susquehanna River. Hunters that avoided roads and harvested deer in these drainages would need to pack the animal uphill to the nearest road.

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. These additional private lands comprised 46% of the total study area in 2006 and contained an extensive road network. Elevation on the study area ranged from 189 m to 723 m.

Tuscarora study area

The Tuscarora study area was located within WMU 4B in the Ridge and Valley physiographic province. This WMU is 64% forested, but only 15% is public land. The ridges supported a mixed-oak hardwood forest dominated by red oak (*Quercus rubra*), white oak (*Quercus alba*), black birch (*Betula lenta*), American beech (*Fagus grandifolia*), yellow poplar (*Liriodendron tulipifera*), white pine (*Pinus strobus*), scarlet oak (*Quercus coccinea*), and chestnut oak (*Quercus prinus;* Cuff et al. 1989). Valleys were predominantly farmland and human developments. Annual snowfall at the Bloserville, Pennsylvania weather station averaged 21.2 inches from 1971-2000 (National Oceanic and Atmospheric Administration 2002). Deer productivity was greater than on the Sproul study area with 170 embryos per 100 adult does, 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 **2-3**). 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, so hunters that harvested deer far from a road often could transport the animal downhill to a vehicle.

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. Elevation on the study area ranged from 102 m to 693 m.

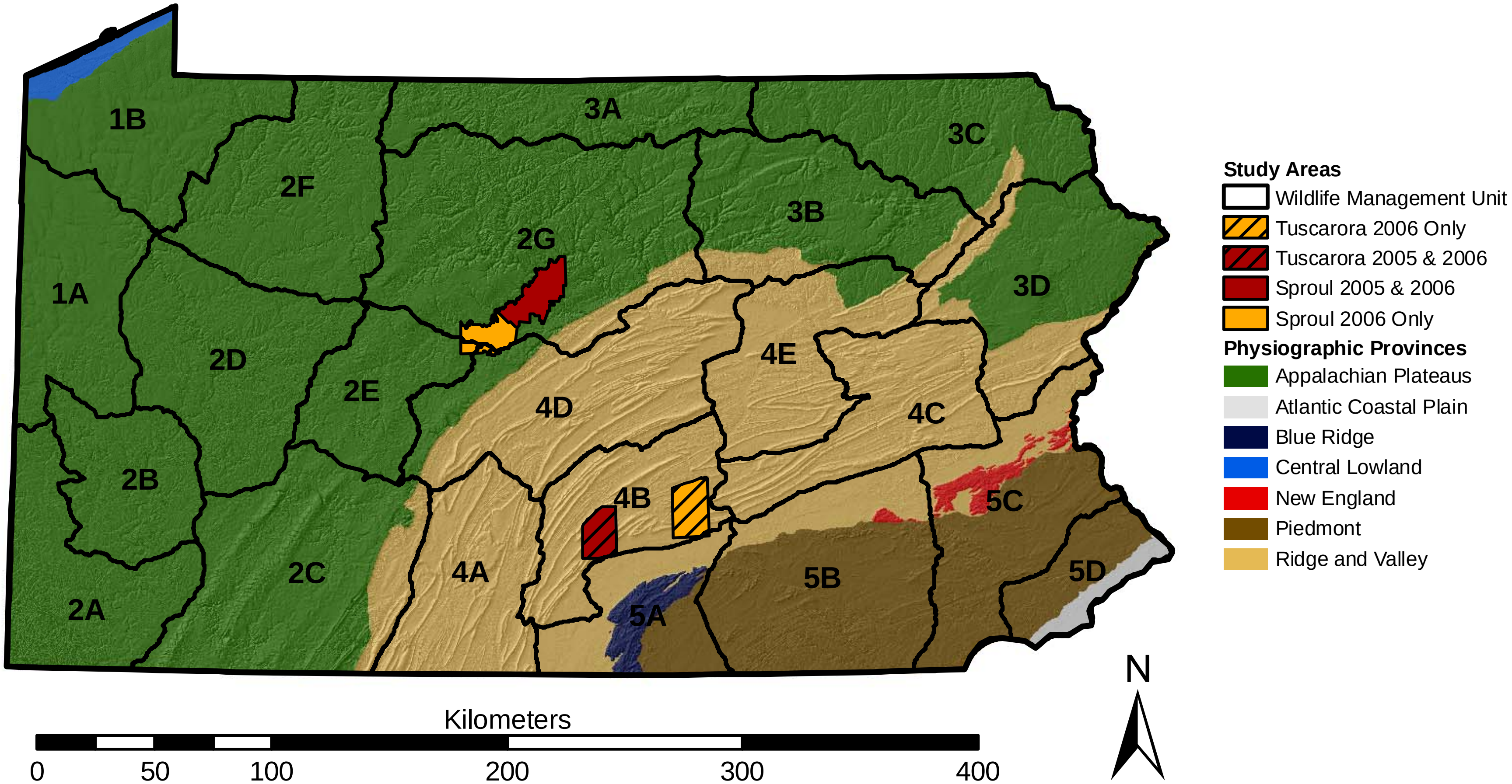

Figure **2-1**: Map of Sproul and Tuscarora study areas. In 2005, deer capture was restricted to mostly public lands on the areas colored in red. In 2006, more deer captures occurred on privately-owned land in the expanded study area colored in orange.

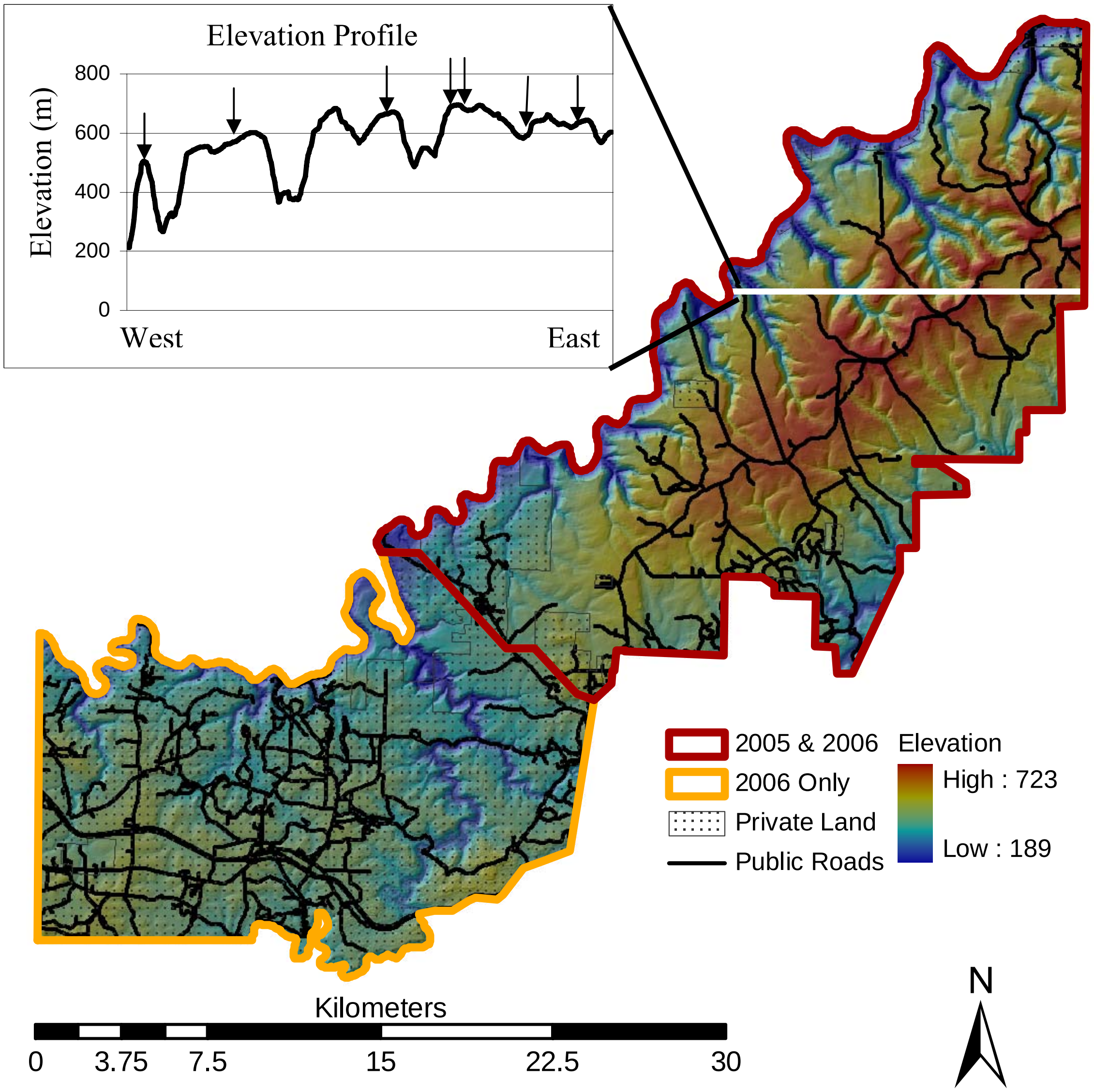

Figure **2-2**: The Sproul study area, located in north-central Pennsylvania in the Allegheny Plateau. The section outlined in orange was added in 2006. Stipples indicate private land ownership. The elevation profile, indicated by the white line, shows that most roads (depicted with black arrows) were located at higher elevations and vehicular access to lower elevations was limited.

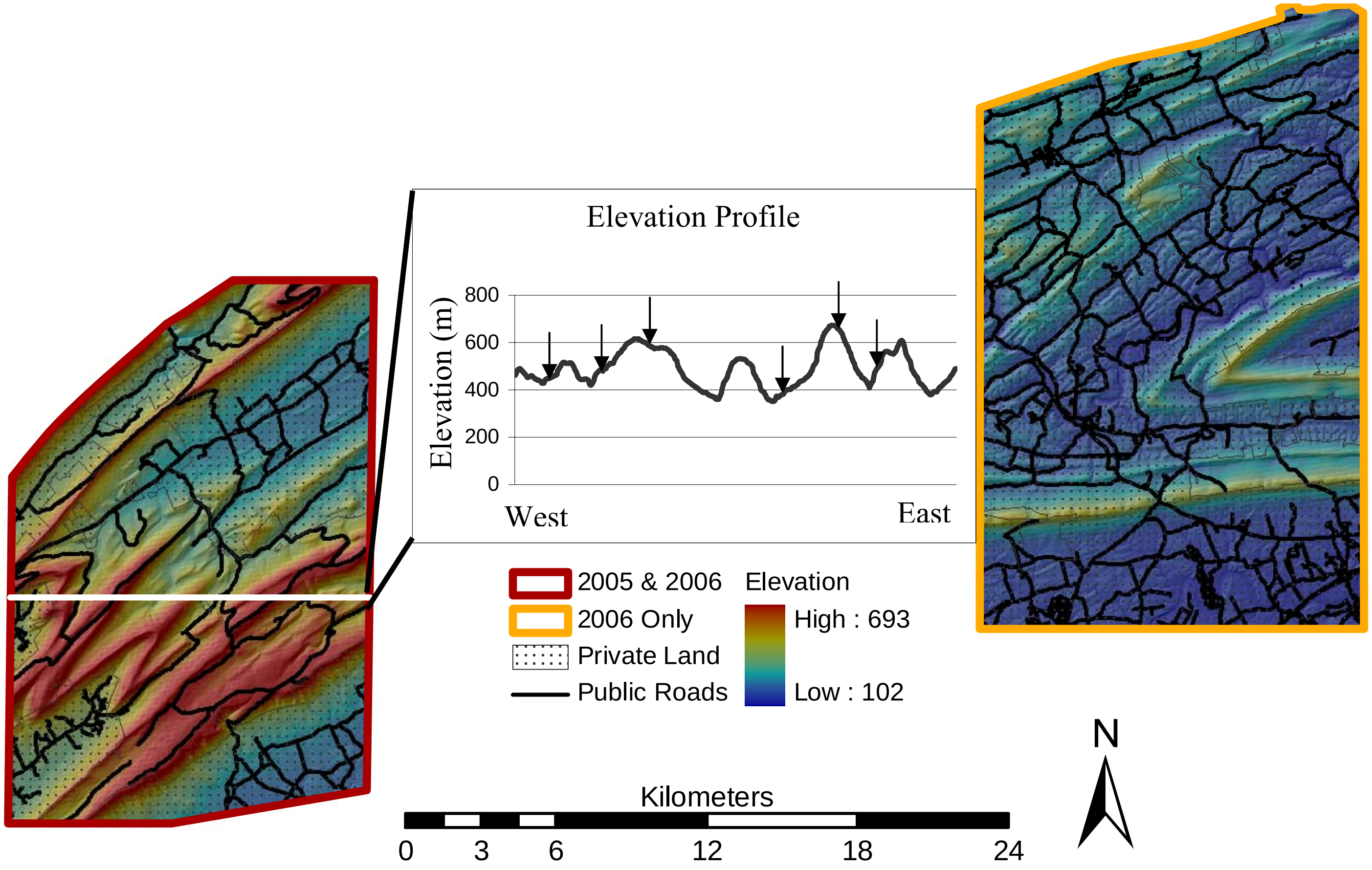

Figure **2-3**: The Tuscarora study area, located in south-central Pennsylvania in the Ridge and Valley Province. The section outlined in orange was added in 2006. Stipples indicate private ownership. The elevation profile, indicated by the white line, shows that roads (depicted with black arrows) were located at both higher and lower elevations.

Chapter 3

Methods

Capture and monitoring of deer

I captured deer January-April of 2005 and 2006 using modified Clover traps (Clover 1954, Beringer et al. 1996, Haulton et al. 2001), drop nets (Ramsey 1968, Conner et al. 1987), and rocket nets (Beringer et al. 1996, Haulton et al. 2001). In August 2006, I 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. The protocols for handling deer were approved by the Pennsylvania State University Institutional Animal Care and Use Committee (IACUC No. 19909).

Corn was the primary bait, but apples, alfalfa, and a mixture of molasses, grains, and minerals also were used occasionally. I set Clover traps close to roads accessible by 4WD vehicles and checked them daily for captures. I 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 (Conner et al. 1987, Haulton et al. 2001). Prior to release, I administered tolazoline hydrochloride at approximately 4.0 mg/kg body weight to reverse the effects of the sedative.

I 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). I fitted subadult females 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). All deer were released at the capture location.

I classified deaths occurring within two weeks of capture as capture myopathy if evidence of any other cause of mortality was lacking. Data from these deer were excluded from data analysis. I 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. I classified deer found dead <100 m from a road, regardless of time since capture, as road-killed if evidence of physical trauma consistent with a vehicle collision was present.

The VHF and GPS collars included circuitry to detect lack of movement and transmit a different radio signal to indicate the deer may have died. Also, VHF collars were equipped with circuitry to transmit a signal indicating time elapsed since the collar entered mortality mode. I monitored all deer for survival once per week during the capture period (approx. 15 January - 15 April), and twice per week the remainder of the year. I investigated mortalities as soon as possible to identify cause of death (Adrian 1996, Vreeland 2002, Bender et al. 2004) and submitted carcasses to The Pennsylvania State University, Animal Diagnosis 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, I 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 some hunters were uncooperative and would discard and sometimes attempt to destroy the radio-collar of legally harvested deer. Therefore, deer that I lost contact with via telemetry during the hunting seasons, and were not found after subsequent ground and aerial searches, I assumed to be legally harvested. Likewise, I assumed radio-collars found with the collar cut and abandoned during a hunting season were legally harvested. If evidence indicated deer were not killed during legal hunting periods, I classified them as illegally killed.

I attempted to estimate the location of each VHF radio-collared female deer twice per week May–December 2005–2006 using ground telemetry triangulation. I 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. I tried to ensure the 95% error ellipse of each location was <1 ha. If I located a collared deer visually, I recorded my 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 a location every 23 hours from date of capture until 15 September, at which time the frequency of estimated locations increased to once per hour.

Aerial surveys of hunters

To estimate hunter density and distribution during the regular rifle season of 2005 and 2006, I used aerial surveys to locate hunters, distance sampling methods to estimate hunter density, and resource selection functions to model hunter distribution (Stedman et al. 2004, Diefenbach et al. 2005). I used two observers to locate hunters from fixed wing aircraft navigating pre-defined transects. I placed transects systematically over the study area from a random starting point and oriented in an 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 occured between 0800 hours and 1100 hours, and afternoon flights from 1330 hours to 1630 hours. Pilots safely navigated >225 m above the high plateaus of the Sproul study area, but flew >525 m above the ridge-and valley topography of the Tuscarora study area. Aircraft maintained airspeeds of approximately 190 km/hr.

I 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. The location of the aircraft was estimated once per second to record the flight path.

Estimating annual survival

I estimated annual survival using the Kaplain-Meier known fates method (Kaplan and Meier 1958) implemented in Program MARK (White and Burnham 1999). The models incorporated weekly fate data from analysis periods 1 May 2005 – 30 April 2006 (study year 2005), and 30 April 2006 – 29 April 2007 (study year 2006). Deer that died or were censored between the date of capture and the analysis period of the same study year were not included in the analysis. I classified deer captured at <1 year of age as subadults and all older deer as adults; subadults captured in 2005 that survived to the following study year were classified as adults in the survival analysis for 2006.

To determine the best model of annual survival, I considered several possible variables. Annual survival may vary seasonally, particularly in relation to hunting seasons (Table **3-1**). This temporal relationship also may vary between study sites or study years (Table **3-2**). In addition, spatial variables such as land ownership and demographic variables such as age may affect annual survival (Table **3-3**). I separately modeled all combinations of these variables and selected the model with the lowest value of Akaike's Information Criterion corrected for sample size (AICc) to estimate annual survival rates, standard errors, and confidence intervals using Program MARK.

Table **3-1**: Temporal variables considered in models of annual survival of antlerless deer on Sproul and Tuscarora study areas, Pennsylvania, USA 2005-06. Each temporal function was modeled with each group effect and each covariate combination listed in tables 3-2 and 3-3, respectively.

Temporal model variables	Description
.	Survival was constant through time.
Month	Survival varied by month.
Hunt, NonHunt	Survival was constant through all hunting seasons (rifle, archery, muzzleloader), and constant outside of hunting seasons.
Rifle, ArchMuzz, NonHunt	Survival was constant during rifle season, constant during archery/muzzleloader seasons, and constant outside of hunting seasons.
Rifle, NonRifle	Survival was constant during rifle season, and constant through all other weeks of the year.
Rifle, ArchMuzz, Wntr, Sumr	Survival was constant during rifle season, constant through archery/muzzleloader seasons, constant through non-hunting weeks from 13 November – 30 April (Wntr), and constant from 1 May – 30 September (Sumr).

Table **3-2**: Study area (Site) and year (Yr) model configurations to estimate annual survival rates of antlerless deer on Sproul and Tuscarora study areas, Pennsylvania, USA 2005-06. Each group effect was modeled with each temporal function and covariate combination listed in tables 3-1 and 3-3, respectively.

Group effect	Description
*Site	Survival function was unique for each study site.
+Site	Survival function had the same slope but different intercepts for each study site.
+Yr	Survival function had the same slope but different intercepts for each study year.
+Site+Yr	Survival function had only one slope, but different intercepts for each study site and study year.
+Yr *Site	Survival function had different slopes for each study site and different intercepts for each study year.

Table **3-3**: Age of deer (AGE = subadult or adult) land ownership (OWNER = proportion of locations on public land), and study site (Site) variables included in candidate models of female white-tailed deer annual survival on the Sproul and Tuscarora study areas, Pennsylvania, USA 2005-06. Each covariate combination was modeled with each temporal function and each group effect listed in tables 3-1 and 3-2, respectively.

Variable	Description
AGE	Survival varies by age of deer.
OWNER	Survival varies by land ownership (public vs. private)
OWNER*Site	The effect of land ownership varies by study area.
AGE+OWNER	Survival varies by age of deer and land ownership.
AGE+OWNER*Site	Survival varies by age of deer and the effect of land ownership varies by study area.

Estimating harvest rate

I estimated the harvest rate on each study area using the known-fates procedure in Program MARK for the 12-week hunting seasons. Only harvests (animals shot and recovered) were entered as deaths in the encounter history and all other mortalities were treated as censored deer. Separate analyses were conducted for each study area.

Harvest rate may differ between rifle and archery/muzzleloader hunting seasons or between study years (Table **3-4**). Also, spatial variables such as land ownership and demographic variables such as age of deer may affect harvest rate (Table **3-5**). I separately modeled all combinations of these temporal functions and covariate effects, and used the model with the lowest AICc to estimate harvest rate. I estimated $\hat{H}$ as

$1-\hat{S}$, where $\hat{S}$ is the survival estimate from Program MARK. A 95% confidence interval (Burnham et al. 1987) was calculated as

$$95\%\ \mathrm{CI} = (\hat{H}/C, \hat{H}*C),$$

$$\mathrm{C} = \exp\left[z_{\alpha/2}\sqrt{\ln(1+\left[cv(\hat{H})\right]^2)} \right]$$

$$\text{And } cv(\hat{H}) = \frac{se(\hat{S})}{\hat{H}}.$$

Table **3-4**: Temporal variables considered in models of harvest rate of female white-tailed deer on the Sproul and Tuscarora study areas, Pennsylvania, USA 2005-06. Each temporal function was modeled with each covariate combination listed in Table 3-5.

Temporal model variables	Description
.	Harvest was constant through hunting seasons and years.
Year	Harvest varied by study year.
Rifle, ArchMuzz	Harvest was constant during the rifle season and constant through archery and muzzleloader seasons.
(Rifle, ArchMuzz)*year	Harvest was constant during the rifle season and constant through archery and muzzleloader seasons, with a unique function for each study year.
(Rifle, ArchMuzz)+year	Harvest was constant during the rifle season and constant through archery and muzzleloader seasons, with the same slope but different intercepts for each year.

Table **3-5**: Spatial and demographic variables included in models of female white-tailed deer harvest rate on the Sproul and Tuscarora study areas, Pennsylvania, USA 2005-06. Each covariate combination was modeled with each temporal function listed in Table 3-4.

Variable	Description
AGE	Harvest varied by age of deer.
OWNER	Harvest varied by land ownership (public vs. private)
AGE+OWNER	Harvest varied by age of deer and land ownership.

Spatial modeling of hunting mortality

I modeled hunting mortality, *K*, as a function of three landscape variables: distance from the nearest road (ROAD), slope of the landscape (SLOPE), and land ownership (OWNER). I defined hunting mortality as deer killed by hunters during the hunting seasons regardless if recovered by the hunter. I used logistic regression (PROC LOGISTIC, SAS Institute, Cary, North Carolina, USA) to estimate *K* (1 = hunting mortality, 0 = otherwise). Deer that died from causes other than hunting were excluded from this analysis.

For each deer, I determined the value of these landscape variables using the most recent 30 telemetry locations acquired during and before the hunting season. Because many of these 30 locations were obtained prior to the hunting season, I visually examined the locations in the GIS for shifts in spatial location. If I detected a shift in locations of a deer, I excluded all locations for that deer prior to when the shift occurred.

I created a grid for each study area with 30 m × 30 m cells containing values for each landscape variable. I calculated ROAD as the linear distance from the center of each cell to the nearest road open to public travel during the hunting season. Roads included state forest roads open to public vehicles (Pennsylvania Department of Conservation and Natural Resources, Bureau of Forestry), as well as municipal and state-maintained roads (Pennsylvania Spatial Data Access, www.pasda.psu.edu). I calculated slope with the Spatial Analyst extension in ArcMap, from a 26 m × 26 m digital elevation model (National Elevation Dataset, U.S. Geological Survey) so that the slope value associated with each cell was an average value derived from the slope of that grid cell and 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 (Pennsylvania Spatial Data Access, accessed 2006) and 0 otherwise. For each deer, I calculated the mean values of ROAD, SLOPE, and OWNER from the grid cells that contained estimated deer locations.

I identified a 95% confidence set of hunting mortality models from eight candidate models (Table **3-6**) using methods outlined in Burnham and Anderson (2002). Starting with the model with the lowest 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 AICc between model *i* and the model with the lowest AICc value. Each time a model was added, the Akaike weights of all models in the set were calculated and summed, until the sum was ≤ 0.95. I then model averaged each coefficient term, $\hat{\beta}_{j,i}$ (coefficient for predictor *j* in model *i*)

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

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

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

I estimated hunting mortality for each 30m × 30m grid cell based on the ROAD, SLOPE, and OWNER values and the $\tilde{\bar{\beta}}$ values. I displayed the spatial variation in estimated hunting mortality on a map of each study area as a chorograph.

Table **3-6**: 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	Description
ROAD	Hunting mortality is a function of the distance from the nearest public road
SLOPE	Hunting mortality is a function of the slope of the landscape
OWNER	Hunting mortality is a function of land ownership (public vs. private)
ROAD+OWNER	Hunting mortality is a function of the distance from the nearest public road and land ownership
SLOPE+OWNER	Hunting mortality is a function of the slope of the landscape and land ownership
ROAD+SLOPE+ROAD*SLOPE	Hunting mortality is a function of the distance from the nearest public road, the slope of the landscape, and the interaction between the two
ROAD+SLOPE+OWNER	Hunting mortality is a function of the distance from the nearest public road, the slope of the landscape, and land ownership
ROAD+SLOPE+ROAD*SLOPE+OWNER	Hunting mortality is a function of the distance from the nearest public road, the slope of the landscape, the interaction between distance from road and slope of the landscape, and land ownership

Estimating hunter density

I estimated hunter density using distance sampling methods and program DISTANCE (Buckland et al. 2001, Stedman et al. 2004, Diefenbach et al. 2005, Thomas et al. 2006). I 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 hunters directly on the flight path, I examined the histogram of observations of hunters by distance from the flight path for each observer to identify a distance at which hunters were not likely to be obscured and assigned this as zero distance. I assumed all hunters were detected at this distance, but <100% of hunters were detected at greater distances.

In 2005 I surveyed public lands almost exclusively (Figures **2-2** and **2-3**) but in 2006 I estimated hunter density separately for public and private land. I classified a transect line as “public” if >50% of the land within the estimated survey strip width was publicly owned. I post-stratified the data by each survey flight to estimate hunter density for each flight. I 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 evaluated for modeling detection functions for each observer and I selected the model with the lowest AICc value.

Spatial modeling of hunter distribution

I modeled hunter distribution with respect to the same landscape variables as hunting mortality for deer (Table **3-7**; see **Spatial Modeling of Hunting Mortality**). Grid cells where hunters were observed were classified as used habitat by hunters. All grid cells were classified as available habitat regardless if they were used by hunters (Manly et al. 2002). I modeled the distribution of hunters as a resource selection function (RSF) for each study area using logistic regression (Manly et al. 2002, Stedman et al. 2004, Diefenbach et al. 2005), where the model predicted relative use by hunters of each grid cell. I used SAS (PROC LOGISTIC; 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**).

I used the model-averaged coefficients to develop the RSF,

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

where $\bar{x}_p$ = average value of covariate p on the landscape. I used the RSF to estimate the relative use of the landscape by hunters for each 30m × 30m grid cell on the study area. I displayed the spatial variation in relative hunter use of each study area on a map as a chorograph.

Table **3-7**: Variables included in models of hunter use on the Sproul and Tuscarora study areas, Pennsylvania, 2005-2006.

Variable	Description
ROAD	Distance from nearest public road (m)
SLOPE	Slope of the landscape (degrees)
OWNER	Land ownership (1 = public, 0 = private)
ROAD^2	Squared distance from the nearest public road (m^2)
SLOPE^2	Squared slope of the landscape (degrees^2)
ROAD*SLOPE	Interaction between distance from road and slope of the landscape
ROAD*OWNER	Interaction between distance from road and land ownership
SLOPE*OWNER	Interaction between slope of the landscape and land ownership

Spatial modeling of hunting efficiency

To identify variations in hunting efficiency across the landscape, I first normalized the hunting mortality ($\hat{K}$) and relative hunter use (RSF) values for each grid cell *i* on public portions of the Sproul Study Area:

$$\overline{\overline{\hat{K}_i}} = \frac{\hat{K}_i - \overline{\hat{K}}}{SD(\hat{K})} \qquad \text{and} \qquad \overline{\overline{RSF_i}} = \frac{RSF_i - \overline{RSF}}{SD(RSF)}.$$

A normalized value of zero indicated that area of the landscape experienced average hunting mortality ($\overline{\overline{\hat{K}_i}}$) or average hunter use ($\overline{\overline{RSF_i}}$), respectively. Positive values represented higher mortality rates or greater hunter use than average and negative values represent lower mortality rates or less hunter use than average.

I estimated hunting efficiency as the difference between the two normalized values ($\overline{\overline{\hat{K}_i}} - \overline{\overline{RSF_i}}$) for each grid cell *i*. A value of zero indicated the hunting mortality rate and hunter use were average; positive values represent locations of greater hunting efficiency and negative values represent locations of lesser hunting efficiency (relative to each parameter's mean value). I displayed spatial variation in hunting efficiency on a map as a chorograph.

Predicting changes in hunting mortality and refugia

I used the hunting mortality model to predict changes in hunting mortality rate that would result from opening more roads to public access on the Sproul study area. Using a GIS layer of all public roads (including gated and unimproved), I estimated new ROAD values for each grid cell on the study area and applied the hunting mortality model (see **Spatial Modeling of Hunting Mortality**) to these data. I calculated the mean hunting mortality rate among all grid cells, $\overline{\hat{K}} = \sum_{i=1}^{n} \hat{K}_i$, where $\hat{K}_i$ = hunting mortality rate for grid cell *i,* as well as the total hectares of *de facto* refugia, $\hat{R} = \frac{\sum N_r \times 9}{100}$, where N_r = number of 30 m × 30 m cells with hunting mortality rate <2%. I estimated the influence of the expanded road network as the change in hunting mortality and refugia:

$$\Delta K = \overline{\hat{K}}_2 - \overline{\hat{K}}_1 \quad \text{and} \quad \Delta P = \hat{P}_2 - \hat{P}_1 \ ,$$

where time period 1 = 2005-06 open road network and time period 2 = expanded road network.

Chapter 4

Results

During 2005-2006, I captured 130 female deer on the Sproul study area and 101 female deer on the Tuscarora study area (Table **4-1**).

Table **4-1**: Number of female deer captured on the Sproul and Tuscarora study areas, Pennsylvania, USA, 2005-2006.

	Sproul Study Area		Tuscarora Study Area	
Year	Subadults	Adults	Subadults	Adults
2005	22	54	26	22
2006	19	35	25	28
Total	41	89	51	50

Hunting was the most common source of mortality for all collared deer but not all causes of mortality were determined (Table **4-2**), 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 I assumed their fate was not related to the failure of the radio-collar.

Table **4-2**: Number of mortalities, by cause of death, for all female white-tailed deer radio-collared, excluding capture-related mortalities, on the Sproul and Tuscarora study areas in Pennsylvania, USA, 2005-2006.

	Sproul Study Area		Tuscarora Study Area	
Cause of mortality	2005	2006	2005	2006
Hunting	4	7	8	14
Unknown	7	3	4	4
Unrecovered hunting[a]	2	0	2	3
Human related[b]	0	4	2	1
Natural causes	1	2	1	1
Illegal kill[c]	0	1	0	0

[a] Deer not recovered by hunters but killed during the hunting season and no evidence that the kill was illegal.
[b] Excluding hunting, most mortalities were vehicle collisions.
[c] Illegal kills included those that occured during the hunting season.

Annual survival

The best model of annual survival rate for 2005 and 2006 included hunting season, land ownership, and study site as explanatory variables (Table **4-3**). Point estimates indicated that on the Sproul study area, annual survival was greater on public land (89.9%, 95% CI = 84.0-96.1%) than private land (75.5%, 95% CI = 66.7-85.6%), but was the opposite on the Tuscarora study area (60.9%, 95% CI = 49.4-75.2% on public land and 75.5%, 95% CI = 66.7-85.6% on private land).

Table **4-3**: Ten top-ranking models of female white-tailed deer annual survival on the Sproul and Tuscarora study areas, Pennsylvania, 2005-06. Survival differed by hunting season (Rifle, ArchMuzz) and was constant outside the hunting seasons (NonHunt) or varied seasonally (Wntr, Sumr). Survival varied also by land ownership (OWNER) and study site (Site). Some models also indicated that survival varied by age of deer (AGE).

Temporal model variables	OWNER, Site, and AGE covariates	Δ AICc	Model weight
Rifle, ArchMuzz, NonHunt	OWNER*Site	0.00	0.24
(Rifle, ArchMuzz, NonHunt) *Site	OWNER*Site	1.17	0.13
Rifle, ArchMuzz, Wntr, Sumr	OWNER*Site	1.34	0.12
(Rifle, ArchMuzz, NonHunt) +Site	OWNER*Site	1.47	0.11
Rifle, ArchMuzz, NonHunt	AGE+OWNER*Site	1.94	0.09
(Rifle, ArchMuzz, NonHunt) +Year	OWNER*Site	2.00	0.09
(Rifle, ArchMuzz, Wntr, Sumr) +Site	OWNER*Site	2.81	0.06
(Rifle, ArchMuzz, Wntr, Sumr) *Site	OWNER*Site	2.89	0.06
(Rifle, ArchMuzz, NonHunt) *Site	AGE+OWNER*Site	3.08	0.05
(Rifle, ArchMuzz, NonHunt) *Site+year	OWNER*Site	3.17	0.05

Harvest rate

The top-ranking harvest rate model for the Sproul study area included a temporal function that allowed harvest to differ between rifle season and archery/muzzleloader seasons and indicated that harvest differed between public and private land (Table **4-4**).

Point estimates indicated harvest rates on private land (16.7%, 95% CI = 8.4-33.2%) were almost four times greater than on public land (4.4%, 95% CI = 1.8-10.8%).

For the Tuscarora study area, the best harvest rate model incorporated temporal variation between the rifle season and archery/muzzleloader seasons, and indicated harvest differed by age (Table **4-5**). Point estimates indicated subadults were harvested at almost twice the rate (30.3%, 95% CI = 19.0-48.1%) as adults (16.4%, 95% CI = 9.4-28.6%).

Because AICc weights were similar among top-ranking models, a model averaging approach to harvest rate estimation may seem warranted. However, the additional variables that the model-average would include (AGE for Sproul and OWNER for Tuscarora, Tables **4-4** and **4-5**), were weak predictors of harvest rate (e.g. <1% difference in harvest between adults and subadults on Sproul's public lands and <4% difference in harvest between public and private land on Tuscarora). Because these differences were not biologically important from a management perspective, and because I was interested in estimating harvest rate as opposed to modeling all potential explanatory variables, I simply estimated harvest rate from the model with the lowest AICc.

Table **4-4**: Ten top-ranking harvest rate models of female white-tailed deer on the Sproul study area, Pennsylvania, USA 2005-06. The best model indicated that harvest differed by hunting season (Rifle; ArchMuzz) and by land ownership (OWNER). Some models indicated that survival varied also by study year (year) or by age of deer (AGE).

Temporal model variables	OWNER and AGE variables	ΔAICc	Model weight
Rifle, ArchMuzz	OWNER	0.00	0.30
Rifle, ArchMuzz + year	OWNER	1.33	0.16
Rifle, ArchMuzz	AGE+OWNER	1.42	0.15
Rifle, ArchMuzz * year	OWNER	2.18	0.10
Rifle, ArchMuzz + year	AGE+OWNER	2.61	0.08
Rifle, ArchMuzz		2.70	0.08
Rifle, ArchMuzz * year	AGE+OWNER	3.48	0.05
Rifle, ArchMuzz + year		4.69	0.03
Rifle, ArchMuzz	AGE	4.70	0.03
Rifle, ArchMuzz * year		5.61	0.02

Table **4-5**: Ten top-ranking harvest rate models of female white-tailed deer on the Tuscarora study area, Pennsylvania, USA 2005-06. The best model indicated that harvest differed by hunting season (Rifle; ArchMuzz) and by age of deer (AGE). Some models indicated that survival varied also by study year (year) or by land ownership (OWNER).

Temporal model variables	OWNER and AGE variables	ΔAICc	Model weight
Rifle, ArchMuzz	AGE	0.00	0.22
Rifle, ArchMuzz		0.76	0.16
Rifle, ArchMuzz	AGE+OWNER	0.81	0.16
Rifle, ArchMuzz + year	AGE	1.97	0.12
Rifle, ArchMuzz	OWNER	1.99	0.09
Rifle, ArchMuzz + year		2.45	0.08
Rifle, ArchMuzz + year	AGE+OWNER	2.64	0.06
Rifle, ArchMuzz * year	AGE+OWNER	3.20	0.04
Rifle, ArchMuzz + year	OWNER	3.48	0.04
Rifle, ArchMuzz * year	AGE	3.87	0.03

Spatial distribution of hunting mortality

No landscape variables that I considered that were related to the spatial distribution of hunting mortality on the Tuscarora study area. On the Sproul study area, the spatial distribution of hunting mortality was related to land ownership, distance from road, and slope (Tables **4-6** and **4-7**, Figures **4-1** and **4-2**). Because model weights were similar among top-ranking models, a model-averaging approach to incorporate all parameters from the 95% confidence set of models was justified. Model-averaging included parameters for ROAD and SLOPE, neither of which were predictors in the top-ranking model. Deer hunting mortality decreased with increasing distance from road, regardless of land ownership. Hunting mortality also decreased with increasing slope, although marginally.

The average hunting mortality rate on public lands in the Sproul study area was 5.6%, although the rate was nearly twice that close to roads (Figure **4-1**). Seventy-four percent of all hunting mortality occurred <500 m from a road, although only 53% of the study area was within that distance. Less than 3% of all hunting mortality occurred in locations >1,200 m from a road, compared to 11% of the study area being within that distance category.

The average hunting mortality rate on private lands on the Sproul study area was 14.5%, and rates were higher close to roads (Figure **4-1**). Eighty-seven percent of all hunting mortality occurred <500 m from a road, compared to 74% of the study area being within that distance category. Only 1% of mortality occurred in locations >1,200 m from a road, although 5% of the study area was within that distance category.

A chorograph of hunting mortality on the landscape showed the spatial variation in hunting mortality on the Sproul study area (Figure **4-3**).

Table **4-6**: Ninety-five percent confidence set of models of hunting mortality of female white-tailed deer on the Sproul study area, Pennsylvania, USA, 2005-06. Hunting mortality varied by land ownership (OWNER), distance from public road (ROAD) and slope of the landscape (SLOPE).

Model	ΔAICc	AICc weight
OWNER	0.00	0.25
ROAD	0.39	0.20
ROAD+OWNER	0.45	0.20
SLOPE+OWNER	1.77	0.10
ROAD+SLOPE	2.33	0.08
ROAD+SLOPE+OWNER	2.45	0.07

Table **4-7**: Final model-average logistic regression parameter and odds ratio estimates of hunting mortality of female white-tailed deer on the Sproul study area, Pennsylvania, USA, 2005-06.

Parameter	$\hat{\beta}$	$SE(\hat{\beta})$	Odds Ratio	95% CI (Odds Ratio)
Intercept	-1.303	0.590		
ROAD (m)	-0.001	0.002	0.999	0.995 - 1.002
SLOPE (degrees)	-0.003	0.035	0.997	0.929 - 1.070
OWNER (public = 1)	-0.817	0.793	0.442	0.090 - 2.158

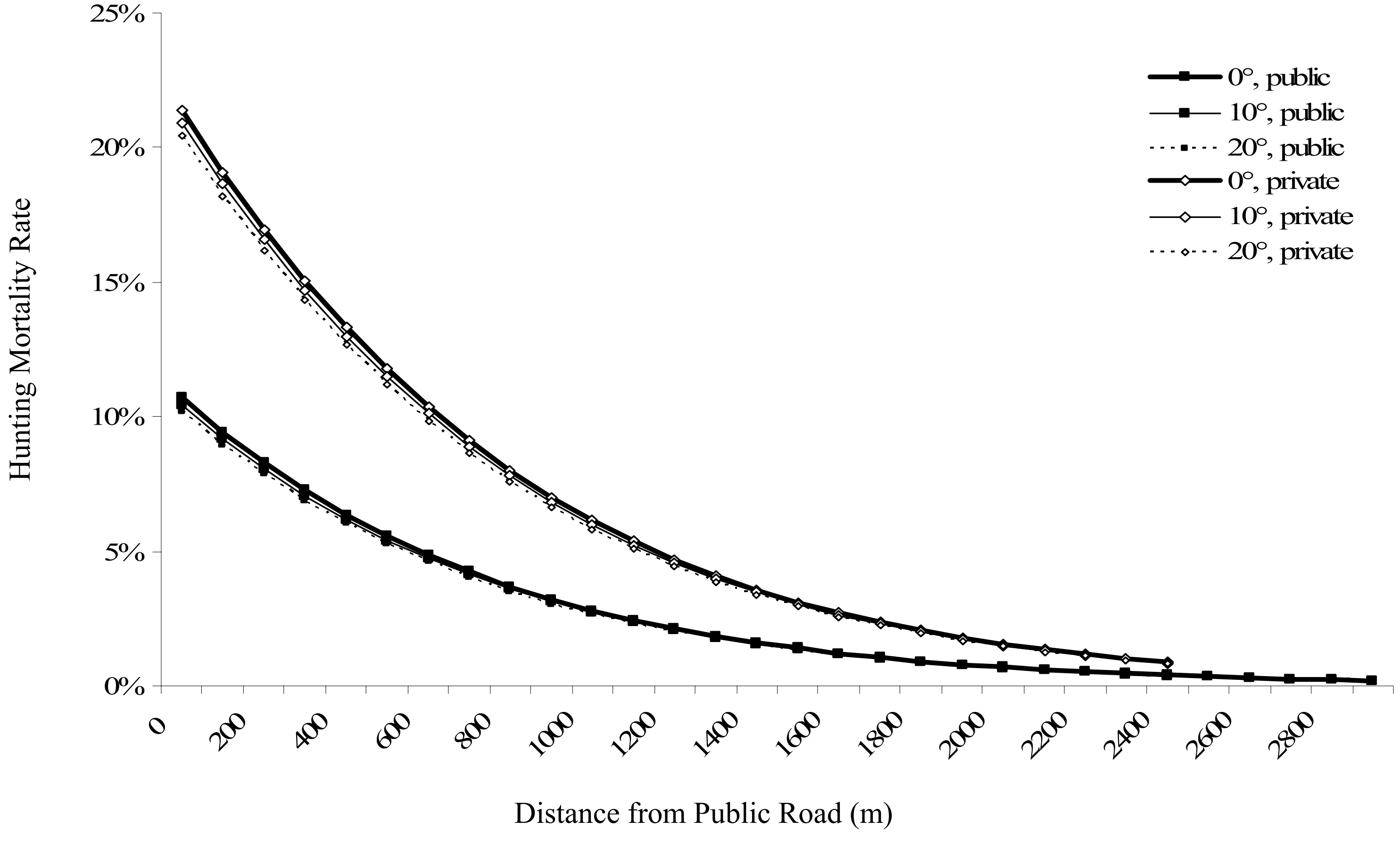

Figure **4-1**: Hunting mortality rate of adult female white-tailed deer in relation to distance from the nearest road and three slopes on the Sproul study area in north-central Pennsylvania, USA 2005-06.

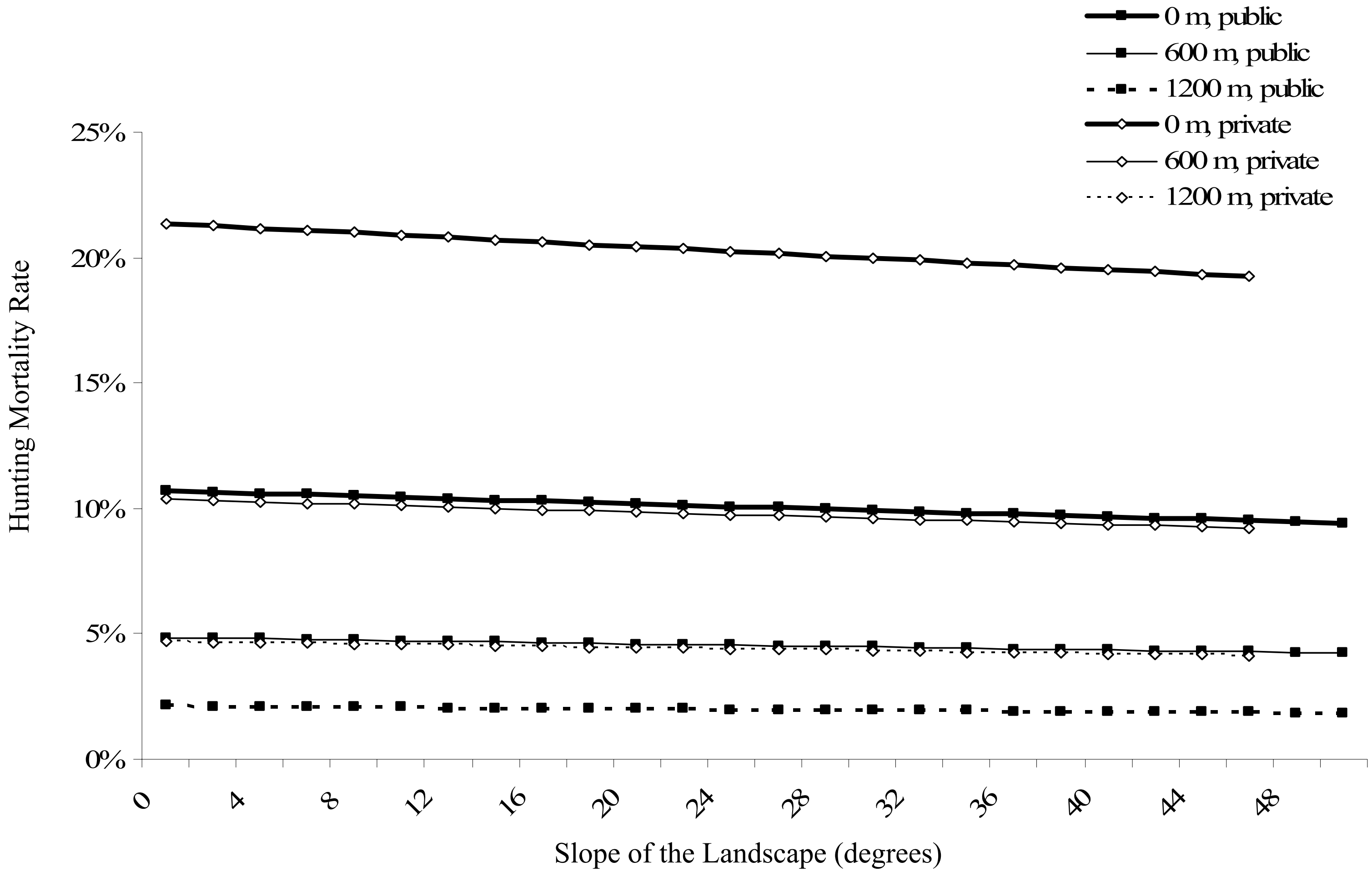

Figure **4-2**: Hunting mortality rate of adult female white-tailed deer in relation to slope of the landscape and three distances from roads on the Sproul study area in north-central Pennsylvania, USA 2005-06.

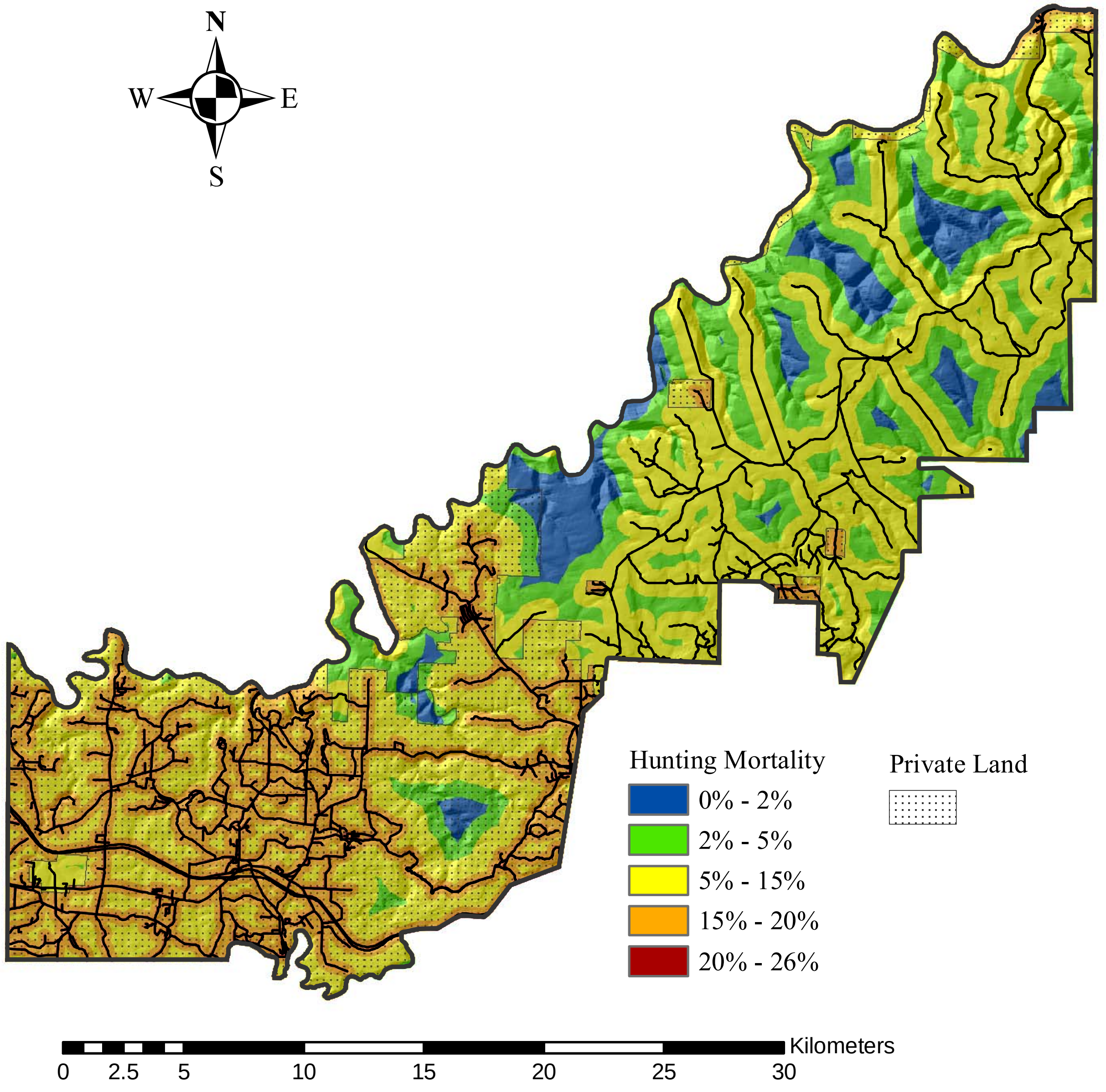

Figure **4-3**: Map representing hunting mortality of female white-tailed deer on the Sproul study area in north-central Pennsylvania, USA 2005-06. Black lines represent roads.

Hunter density

In 2005, adverse weather conditions prevented me from conducting surveys on either the first or second day of the rifle season, and I was 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 **4-4**). Density declined on following days until the first Saturday morning. Hunter densities the second week were lower and remained <0.1 hunters/km^2 until the last Saturday.

In 2006, favorable weather conditions allowed me to conduct hunter surveys during the first three days of the hunting season and on both Saturdays. On public land on the Sproul study area, hunter density was greatest during opening morning (Monday) of rifle season, with 1.1 hunters/km^2 (Figure **4-5**). Hunter densities were <0.4 hunters/km^2 every day from Wednesday afternoon until the end of hunting season. Hunter densities on private lands on the Sproul study area were similar to public lands (1.0-1.1 hunters/km^2 on opening days; Figure **4-6**). Hunter density during the second week of rifle season remained <0.2 hunters/km^2.

In contrast to hunter density on public land on the Sproul study area, hunter density on public land on the Tuscarora study area increased during the first three hunts of 2006, from 0.9 to 1.1 to 1.2 hunters/km^2 during Monday morning, Monday afternoon, and Tuesday morning, respectively (Figure **4-5**). Hunter densities were <0.3 hunters/km^2 during the second week. Hunter densities on private land on the Tuscarora study area decreased from 0.5 to 0.4 to 0.3 hunters/km^2 during Monday morning, Monday afternoon, and Tuesday morning, respectively (Figure **4-6**). Hunter density was <0.3 hunters/km^2 during the remainder of the week.

Spatial distribution of hunters

Results of the spatial distribution of hunters are limited to the 2006 hunting season because more data were collected during that study year, including hunter observations from the first two days of the hunting season and on both private and public land.

Hunter distribution on the Sproul and Tuscarora study areas differed on public and private lands and was related to distance from road and slope (Tables **4-8** - **4-11**). On the Sproul study area, hunter use on public land declined with increasing distance from the road and increasingly steeper slopes (Figures **4-7** and **4-8**). In contrast, on private land, distance from road had little effect on hunter use; hunters on private land tended to use flatter slopes similar to hunters on public land.

Seventy-three percent of hunters on public land on the Sproul study area were located <600 m from a road, compared to 60% of the study area being within that distance (Figure **4-9**). Similarly, 70% of all hunters were located on slopes <8° on public land, which represents 57% of the study area (Figure **4-10**). Hunters on private land were relatively uniformly distributed by distance from road (Figure **4-11**), but 79% of hunters were on slopes <8°, which represents 73% of the study area (Figure **4-12**).

A chorograph of hunter distribution on the landscape shows the spatial distribution of relative hunter use on the Sproul study area (Figures **4-13**).

On the Tuscarora study area, hunters on public land were closer to roads (Figure **4-14)** and 79% of all public land hunters remained <600 m from a road, compared to 69% of the study area being within that distance (Figure **4-16**). Also, hunters tended to avoid steeper slopes but the effect was not as great as on the Sproul study area (Figures **4-15** and **4-17**). Hunters on private land avoided locations both near and far from roads and slope had little effect on the distribution of hunters (Figures **4-14** and **4-15**).

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 on private land very close to roads (Figure **4-20**). Unlike the Sproul study area, there were few large, contiguous areas of lower hunter density.

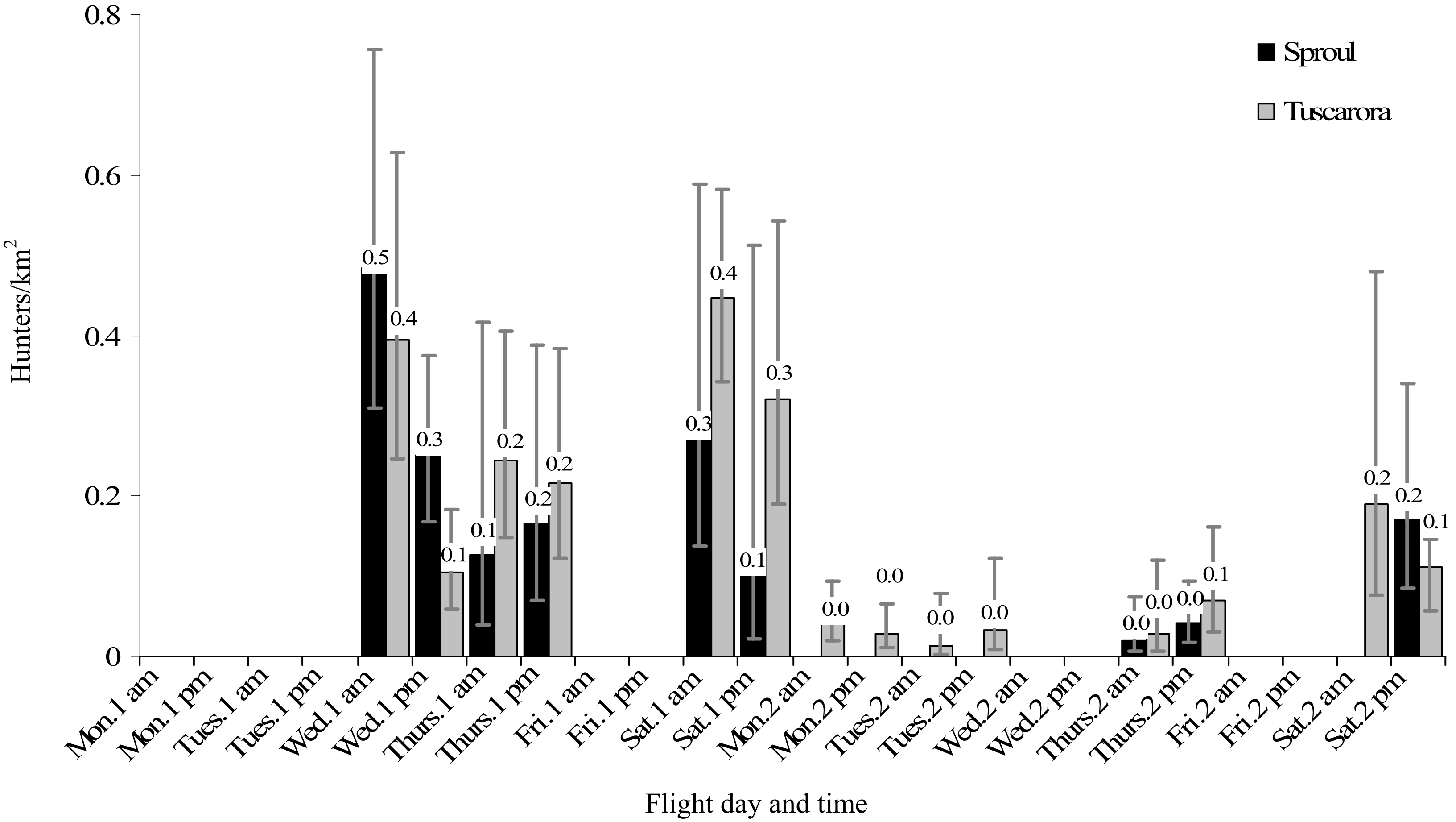

Figure **4-4**: Density (and 95% confidence intervals) of deer hunters on the Sproul and Tuscarora study areas, Pennsylvania, USA during the two-week regular deer rifle season, 28 November – 10 December, 2005. Flights days with no data experienced adverse weather conditions. There is no deer hunting on Sunday in Pennsylvania.

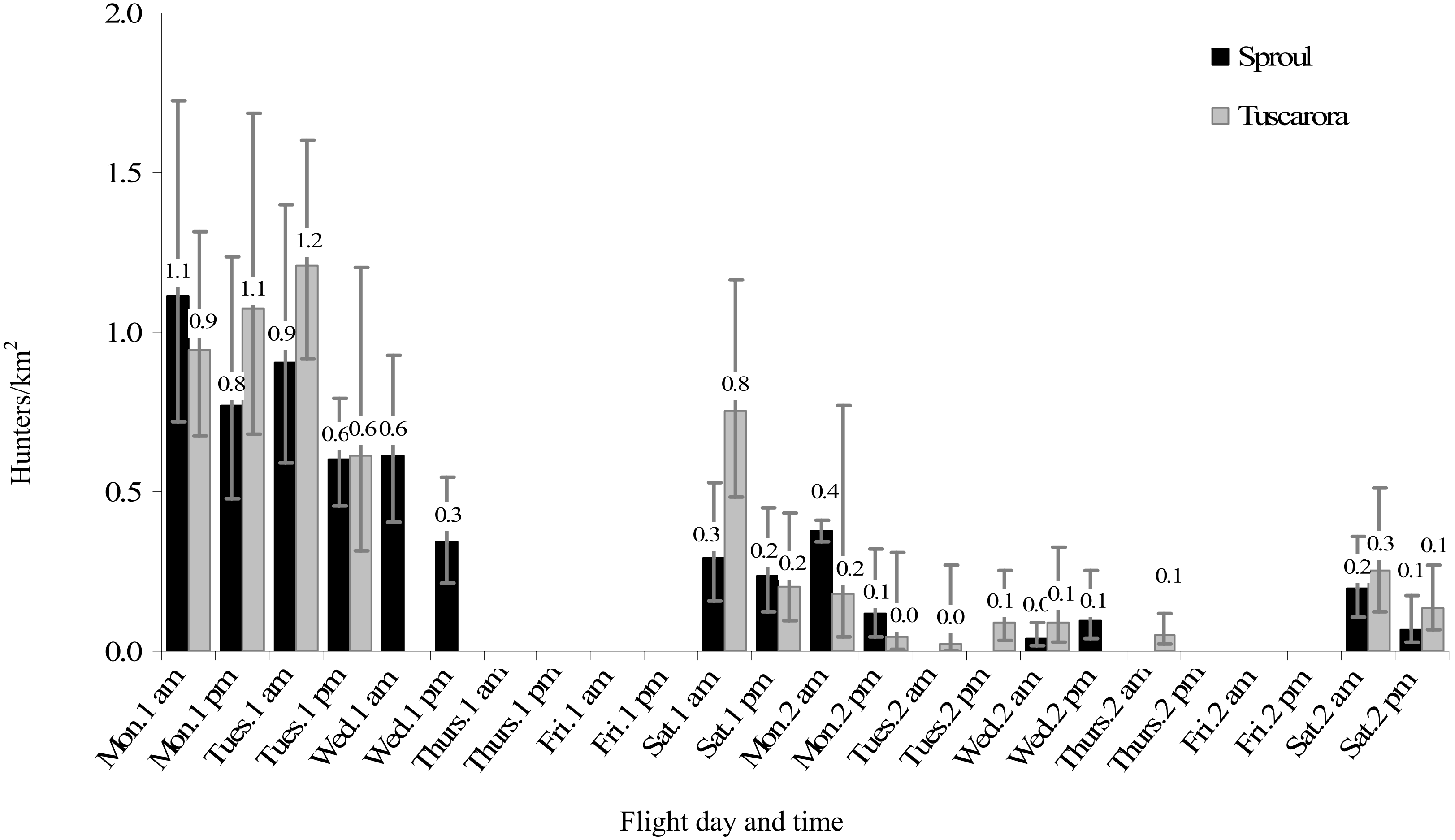

Figure **4-5**: Density (and 95% confidence intervals) of deer hunters on the public land portions of the Sproul and Tuscarora study areas, Pennsylvania, USA during the two-week regular deer rifle season, 4-16 December 2006. Flights days with no data experienced adverse weather conditions. There is no deer hunting on Sunday in Pennsylvania.

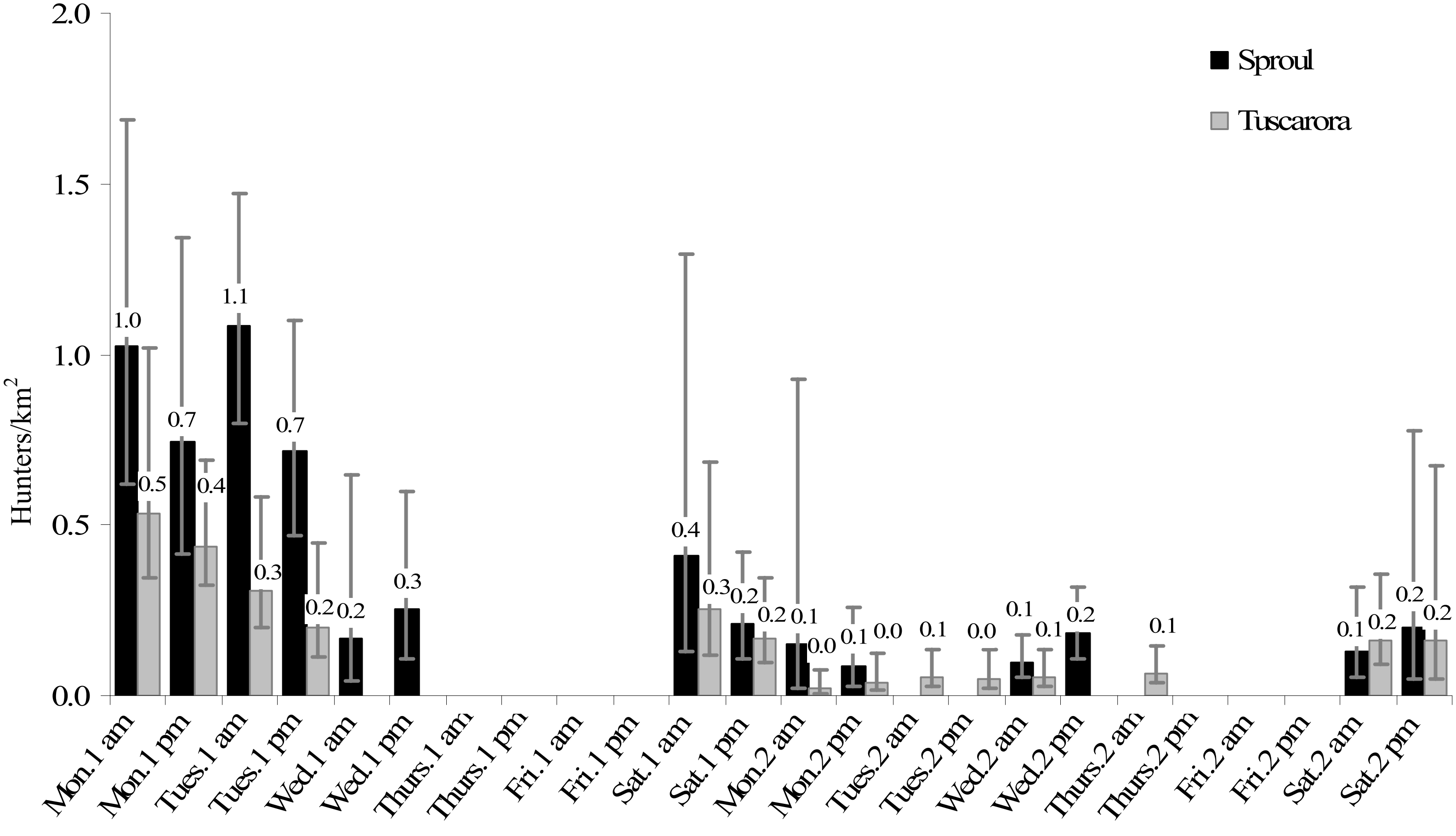

Figure **4-6**: Density (and 95% confidence intervals) of deer hunters on the private land portions of the Sproul and Tuscarora study areas, Pennsylvania, USA during the two-week regular deer rifle season, 4-16 December 2006. Flights days with no data experienced adverse weather conditions. There is no deer hunting on Sunday in Pennsylvania.

Table **4-8**: 95% confidence set of models of spatial distribution of hunters on the Sproul study area, Pennsylvania, USA, 2006. Relative hunter use varied by distance from road (ROAD), slope of the landscape (SLOPE), and land ownership (OWNER).

Model variables	Δ AICc	AICc *w*
ROAD, SLOPE, OWNER, DISTANCE*OWNER	0	0.39
ROAD, SLOPE, OWNER, SLOPE^2, ROAD*OWNER	1.04	0.23
ROAD, SLOPE, OWNER, ROAD*SLOPE, ROAD*OWNER	1.88	0.15
ROAD, SLOPE, OWNER, ROAD*OWNER, SLOPE*OWNER	1.89	0.15
ROAD, SLOPE, OWNER, SLOPE^2, ROAD*SLOPE, ROAD*OWNER	3.02	0.09

Table **4-9**: Model-average of spatial distribution of hunters on the Sproul study area, Pennsylvania, USA, 2006.

Parameter	$\hat{\beta}$	$SE(\hat{\beta})$
Intercept	-6.3700000	0.0752000
ROAD (m)	0.0000415	0.0001230
SLOPE (degrees)	-0.0285000	0.0101000
OWNER (public = 1)	0.5230000	0.0861000
SLOPE^2	-0.0001430	0.0002760
ROAD*SLOPE	-0.0000006	0.0000030
ROAD*OWNER	-0.0005740	0.0001520
SLOPE*OWNER	-0.0005240	0.0020500

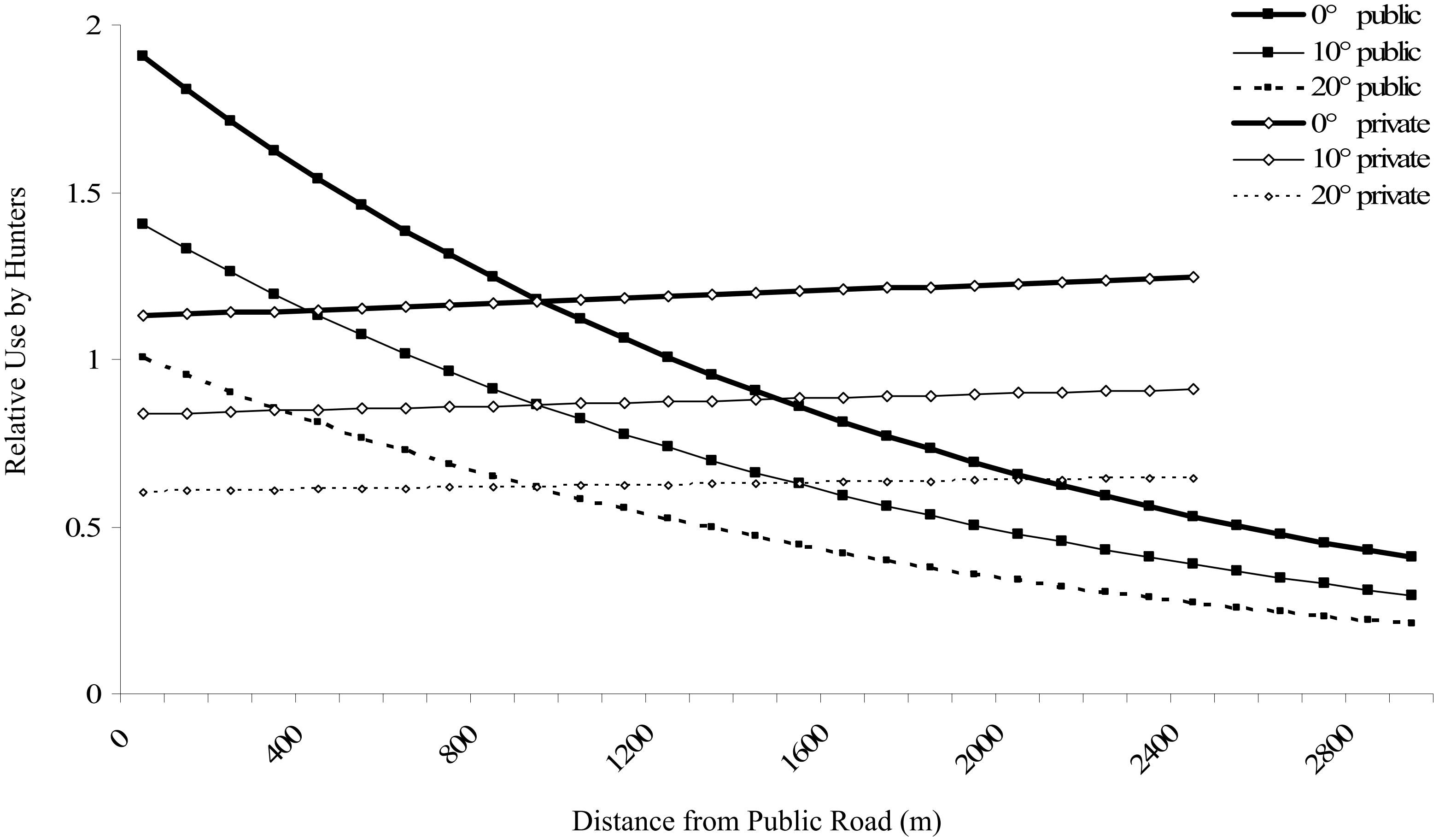

Figure **4-7**: Hunter use as a function of distance from the nearest road for different slopes on Sproul study area, Pennsylvania, USA, 2006. A relative use value of 1 represents hunter use at the average distance and slope of the study area.

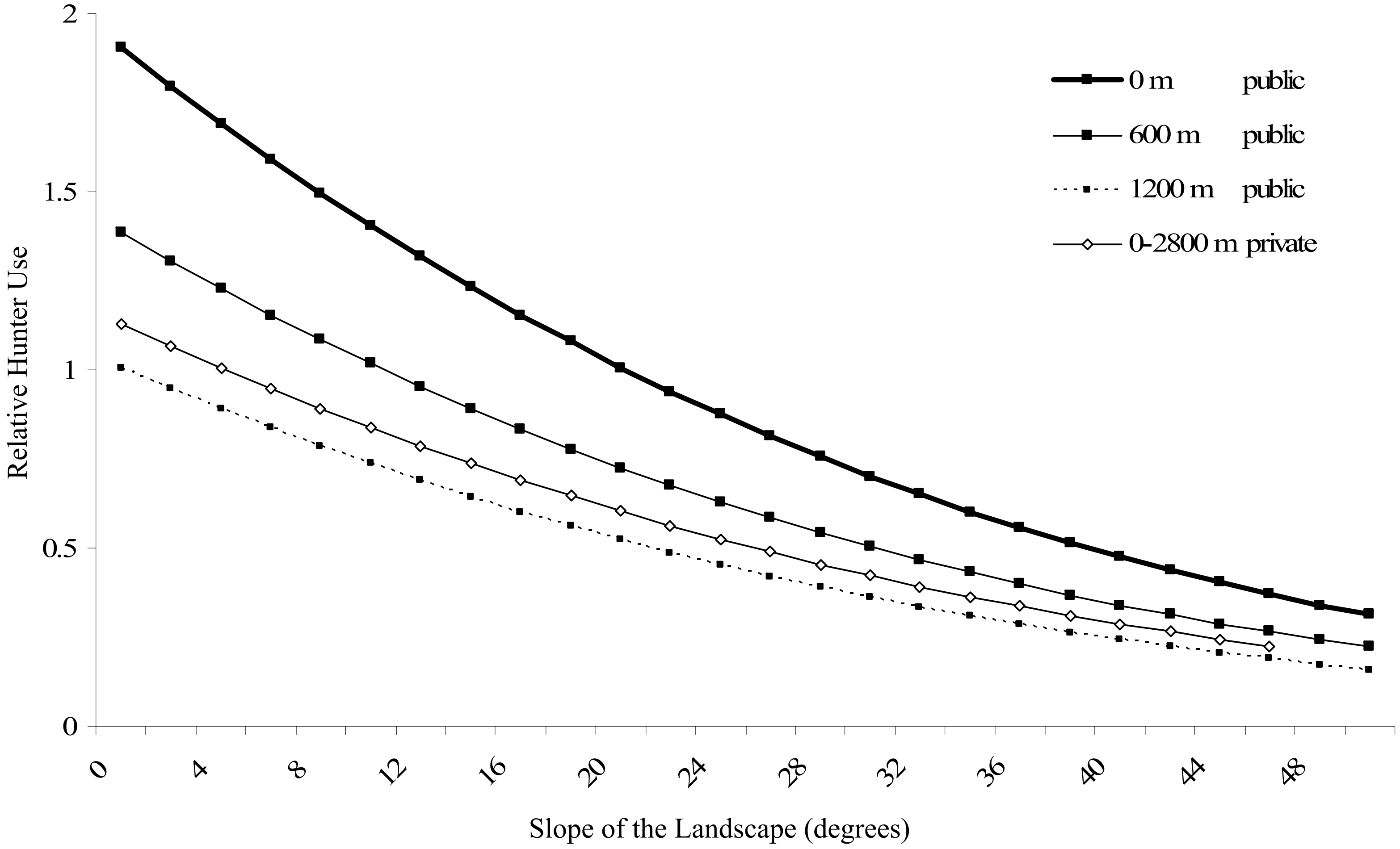

Figure **4-8**: Hunter use as a function of slope for various distances from the nearest road on Sproul study area, Pennsylvania, USA, 2006. A relative use value of 1 represents hunter use at the average distance and slope of the study area.

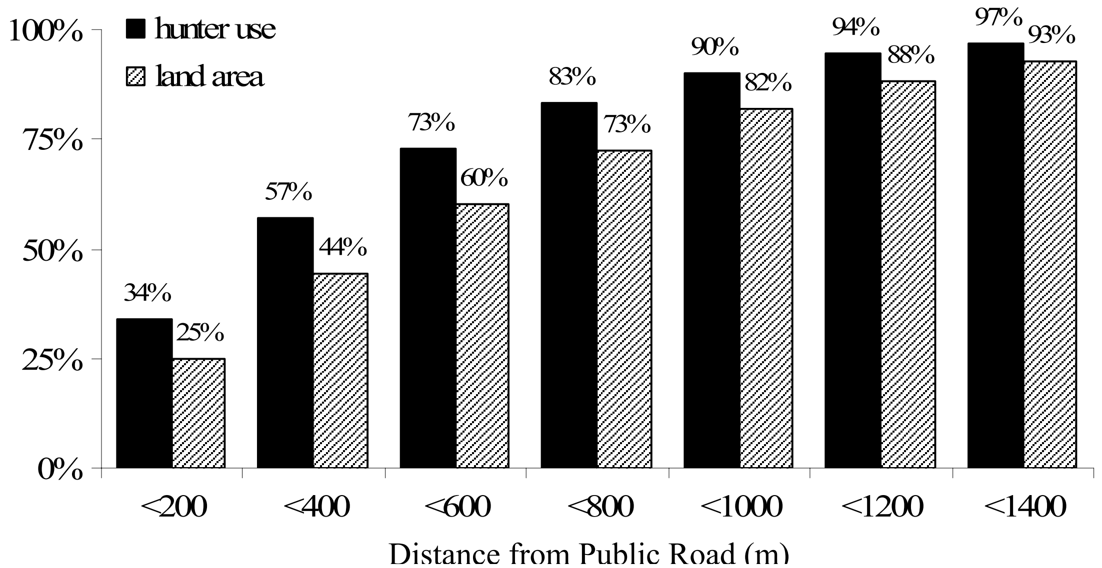

Figure **4-9**: Cumulative distribution of hunters compared to available land area at various distance categories from roads open to the public on public land on the Sproul study area, Pennsylvania, USA, 2006.

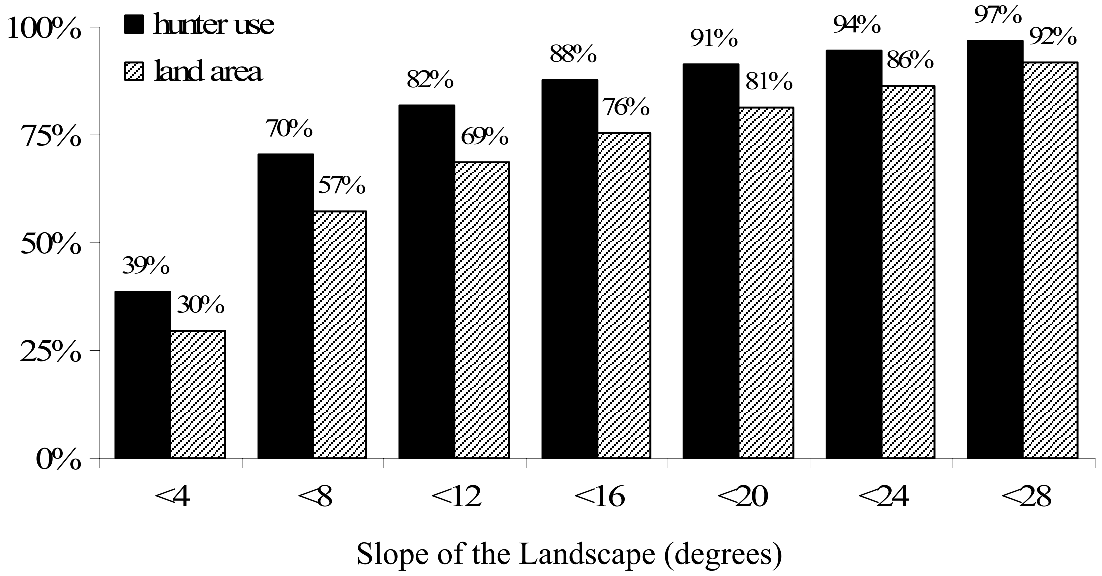

Figure **4-10**: Cumulative distribution of hunters compared to available land of various slopes on public land on the Sproul study area, Pennsylvania, USA, 2006.

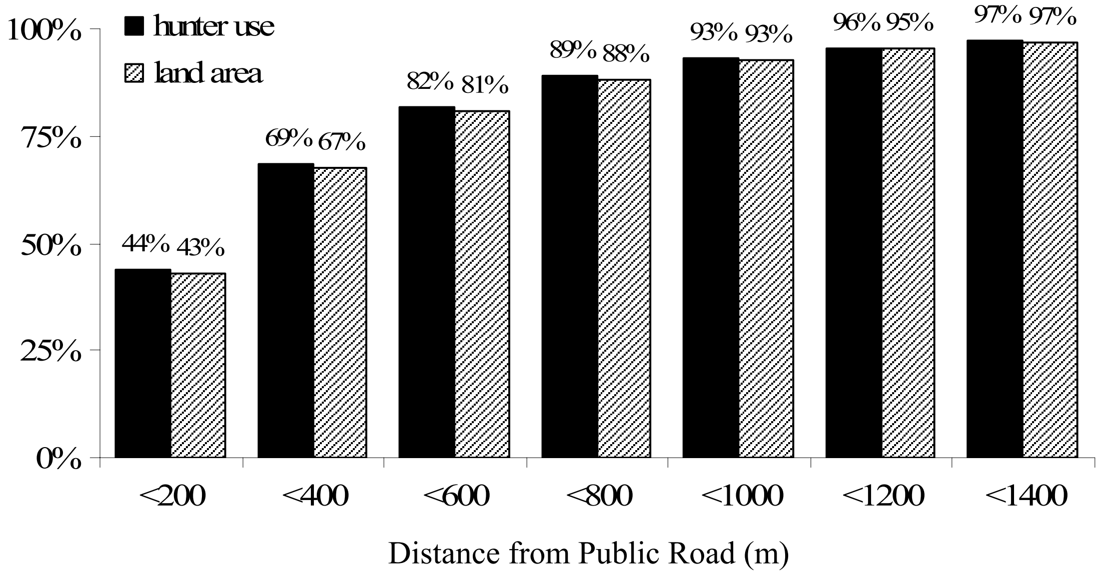

Figure **4-11**: Cumulative distribution of hunters compared to available land area at various distance categories from roads open to the public on private land on the Sproul study area, Pennsylvania, USA, 2006.

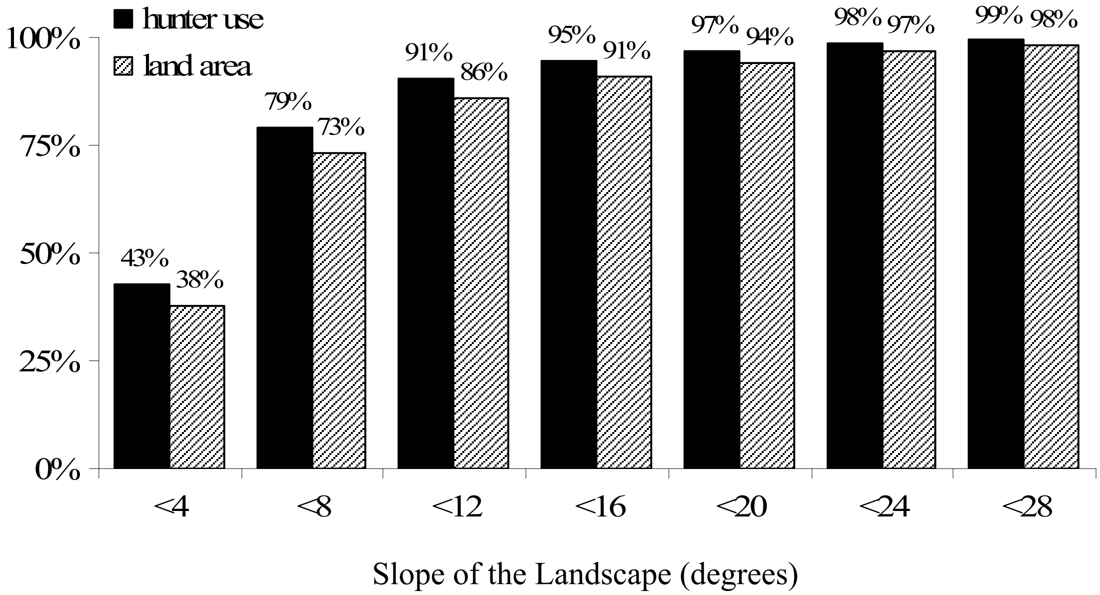

Figure **4-12**: Cumulative distribution of hunters compared to available land of various slopes on private land on the Sproul study area, Pennsylvania, USA, 2006.

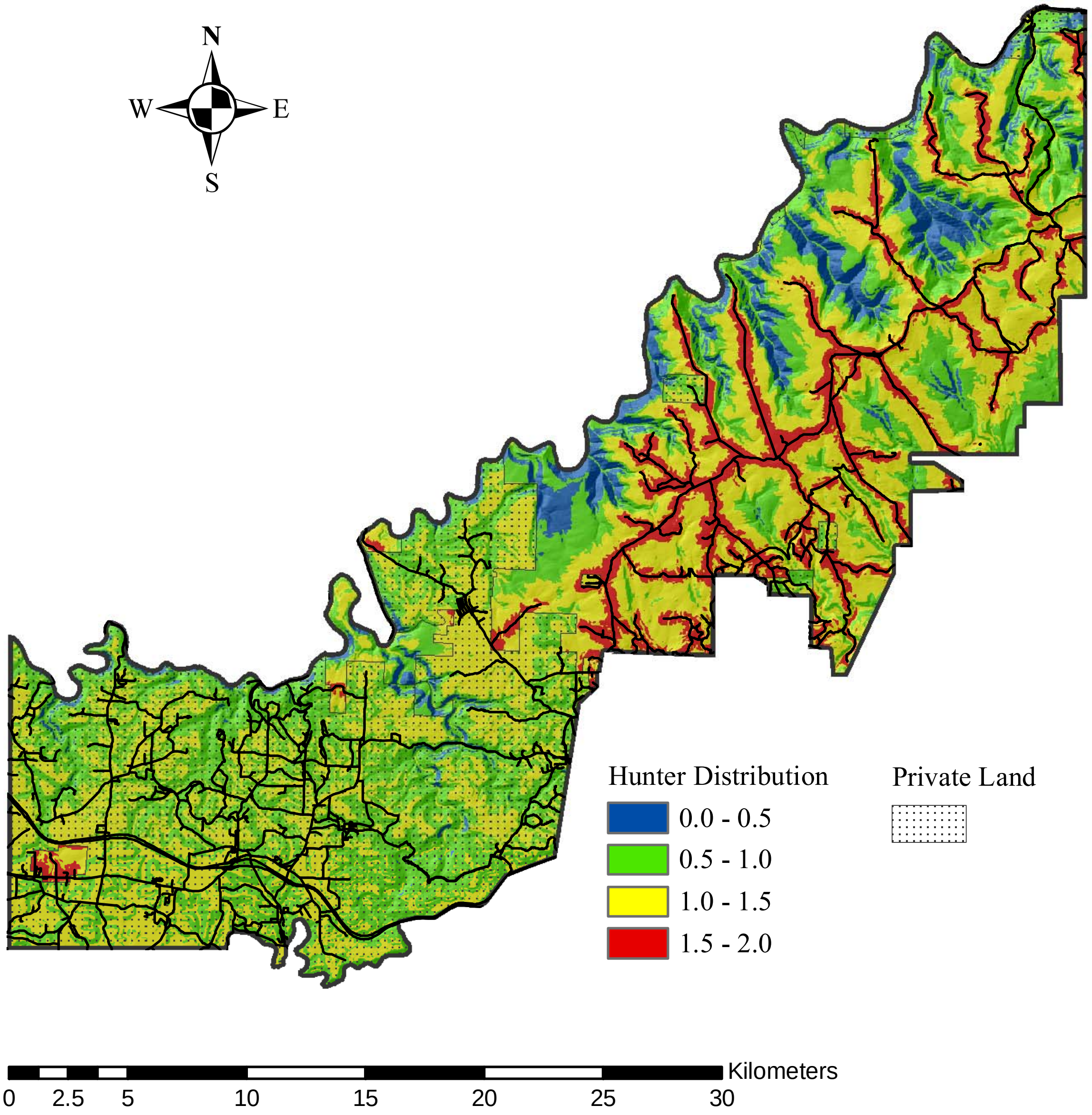

Figure **4-13**: Hunter distribution (relative hunter use) on the Sproul study area in Pennsylvania, USA, 2006. Average hunter use for the study area is represented by a value of 1. Black lines represent roads. Hillshading is used to emphasize topographic relief.

Table **4-10**: 95% confidence set of models of spatial distribution of hunters on the Tuscarora study area, Pennsylvania, USA, 2006. Relative hunter use varied by distance from road (ROAD), land ownership (OWNER), and slope of the landscape (SLOPE).

Model	Δ AICc	AICc *w*
ROAD, OWNER, ROAD^2, ROAD*OWNER	0	0.53
ROAD, SLOPE, OWNER, ROAD^2, ROAD*OWNER	1.98	0.20
ROAD, SLOPE, OWNER, ROAD^2, ROAD*OWNER, SLOPE*OWNER	3.12	0.11
ROAD, SLOPE, OWNER, ROAD^2, ROAD*SLOPE, ROAD*OWNER	3.75	0.08
ROAD, SLOPE, OWNER, ROAD^2, SLOPE^2, ROAD*OWNER	3.92	0.08

Table **4-11**: Model-average of spatial distribution of hunters on the Tuscarora study area, Pennsylvania, USA, 2006.

Parameter	$\hat{\beta}$	$SE(\hat{\beta})$
Intercept	-7.3500000	0.1010000
ROAD (m)	0.0017700	0.0003450
SLOPE (degrees)	0.0026600	0.0073400
OWNER (public=1)	1.3400000	0.1410000
ROAD^2	-0.0000011	0.0000003
SLOPE^2	-0.0000255	0.0000757
ROAD*SLOPE	-0.0000016	0.0000036
ROAD*OWNER	-0.0012800	0.0002400
SLOPE*OWNER	-0.0046200	0.0083700

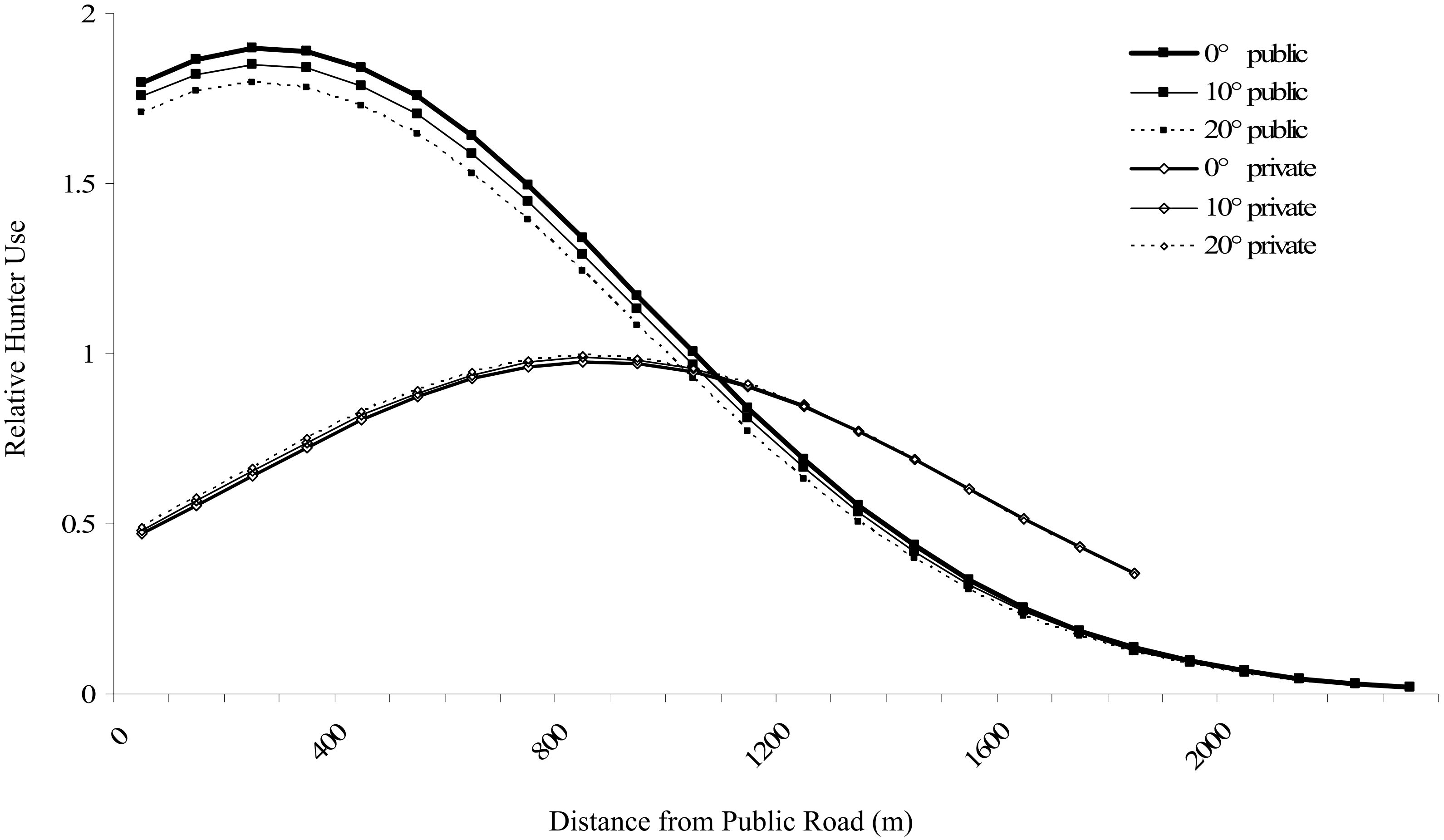

Figure **4-14**: Relative hunter use as a function of distance from nearest public road on the Tuscarora study area, Pennsylvania, USA, 2006. A relative hunter use value of 1 represents hunter use at the average distance and slope of the study area.

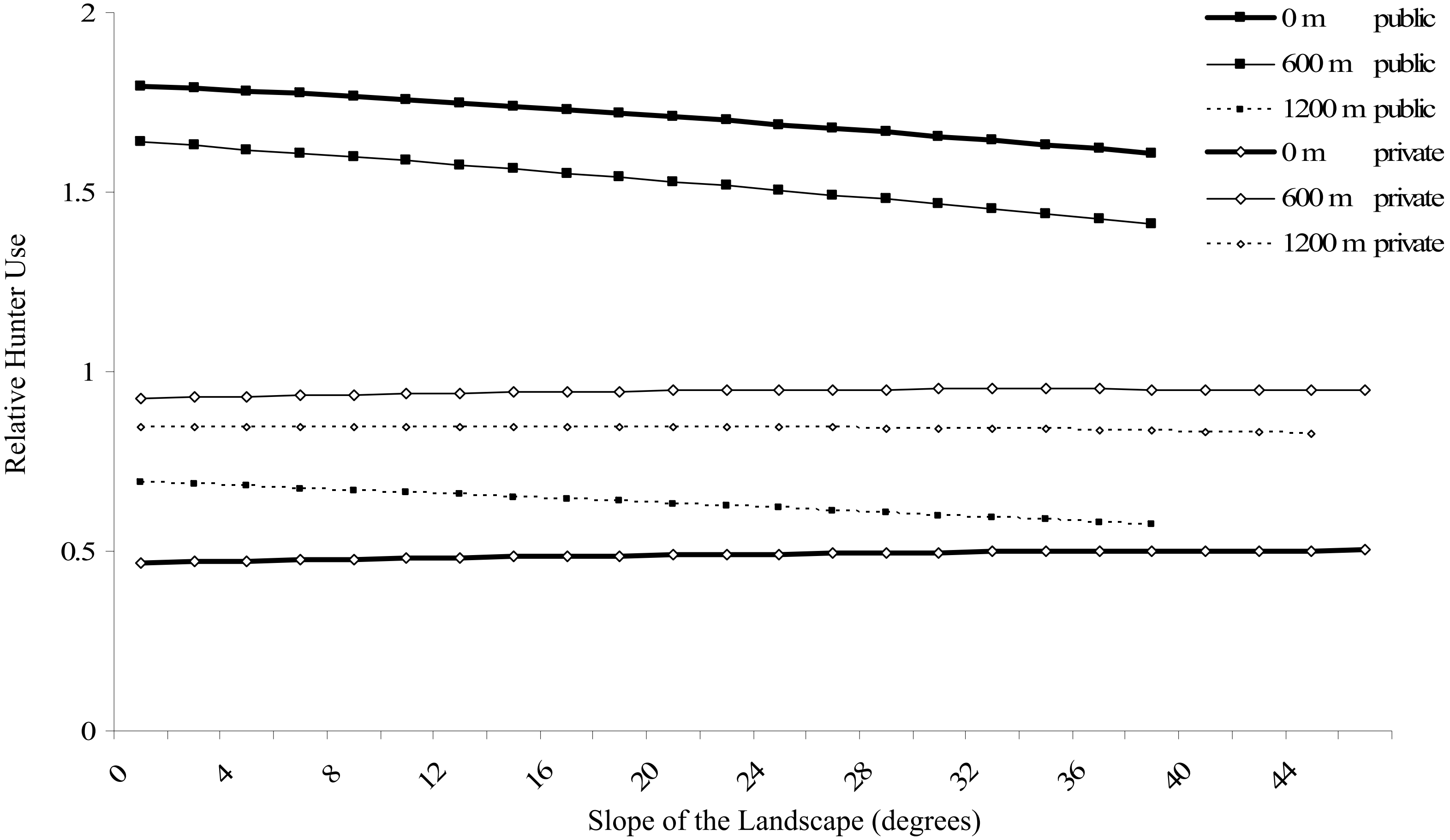

Figure **4-15**: Relative hunter use as a function of slope for various distances from the nearest public road on the Tuscarora study area, Pennsylvania, USA, 2006. A relative hunter use value of 1 represents hunter use at the average distance and slope of the study area.

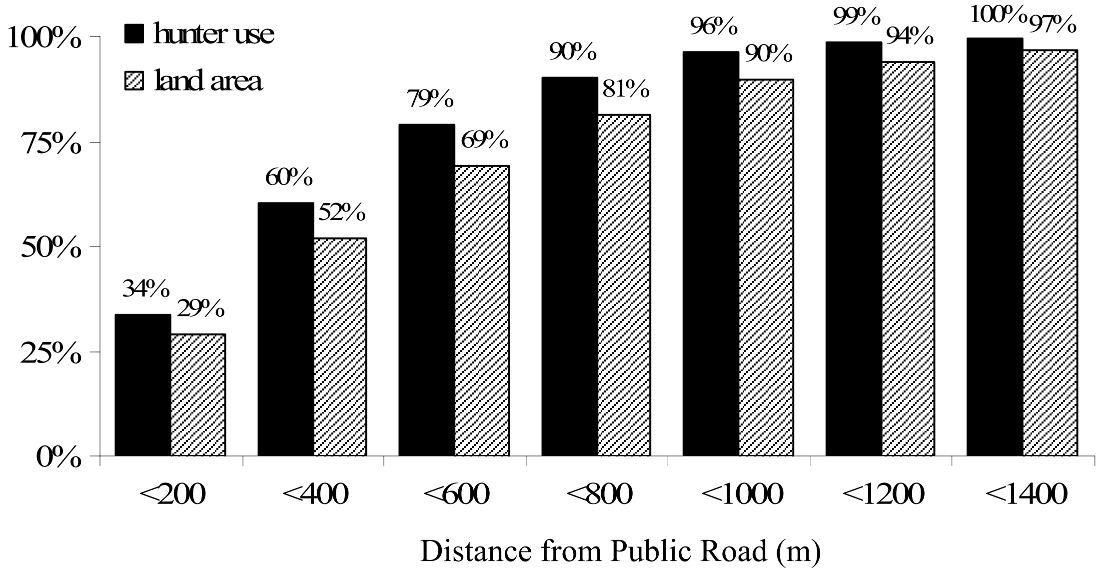

Figure **4-16**: Cumulative distribution of hunters compared to available land according to distance from the nearest road on public land on the Tuscarora study area, Pennsylvania, USA, 2006.

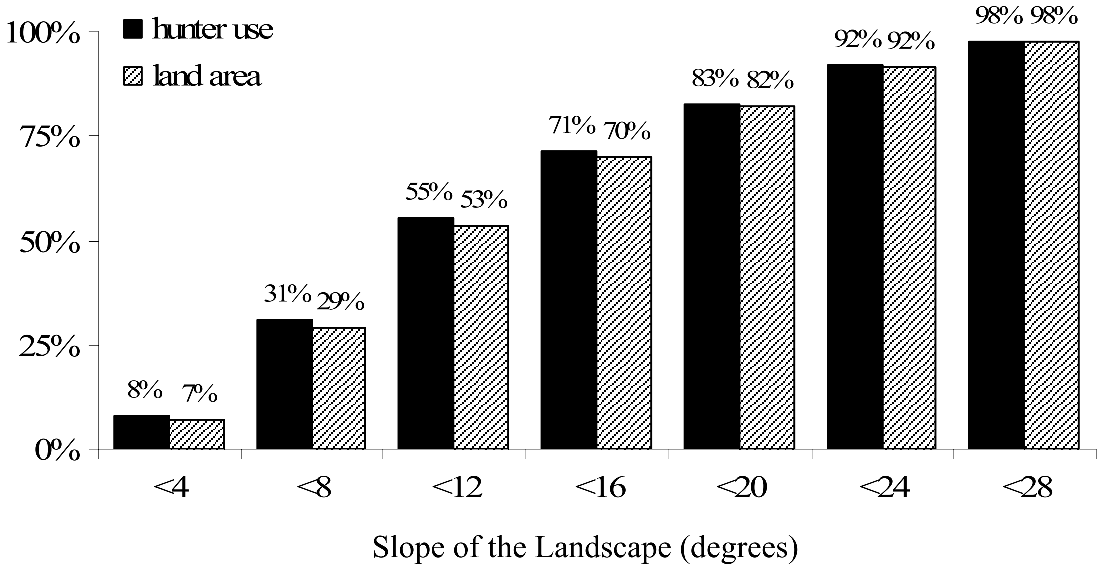

Figure **4-17**: Cumulative distribution of hunters compared to available land according to slope of public land on the Tuscarora study area, Pennsylvania, USA, 2006.

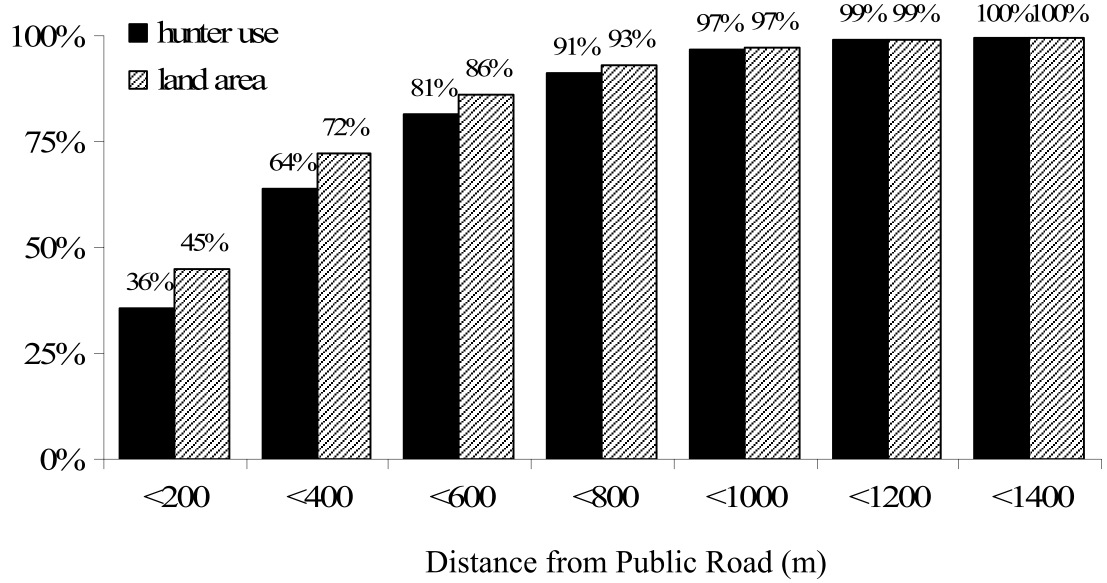

Figure **4-18**: Cumulative distribution of hunters compared to available land according to distance from the nearest public road on private land on the Tuscarora study area, Pennsylvania, USA, 2006.

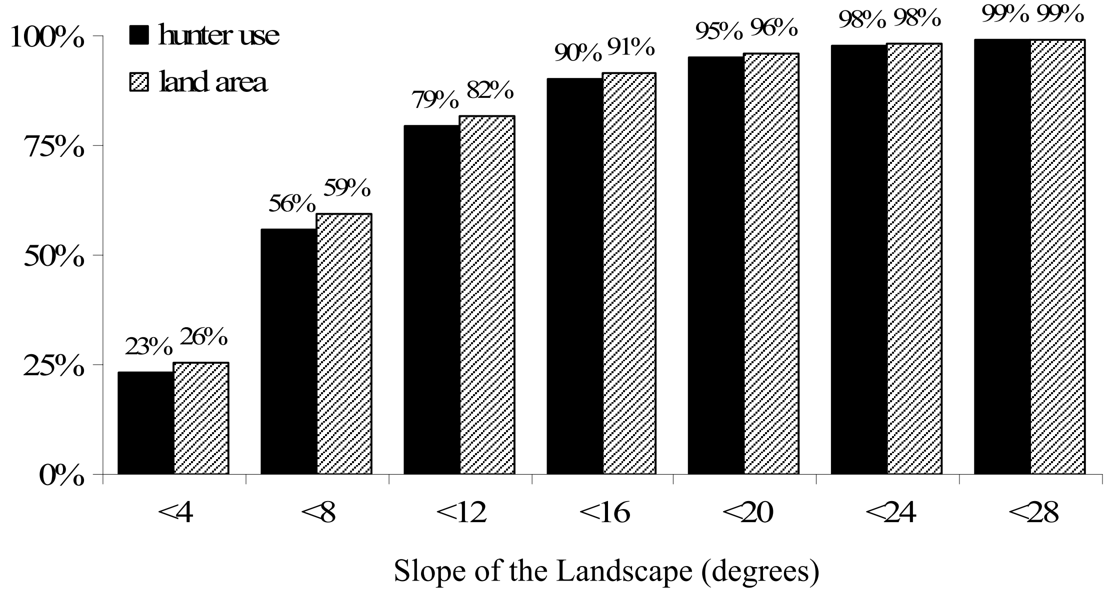

Figure **4-19**: Cumulative distribution of hunters compared to available land according to slope of private land on the Tuscarora study area, Pennsylvania, USA, 2006.

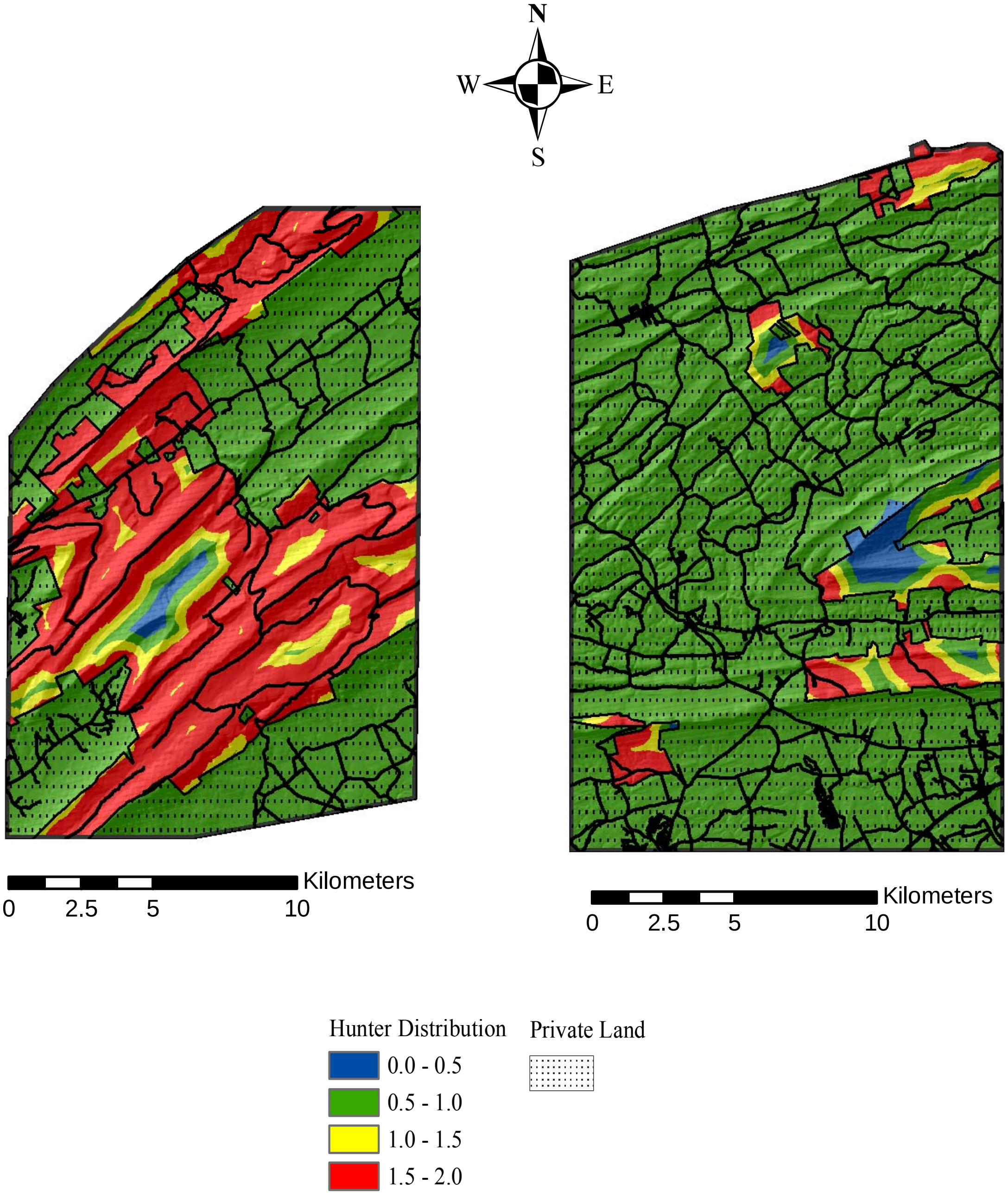

Figure **4-20**: Relative hunter distribution on the Tuscarora study area, Pennsylvania, USA, 2006. Average relative hunter use for the study area is represented by a value of 1. Black lines represent roads. Hillshading is used to emphasize topographic relief.

Spatial distribution of hunting efficiency

Because I did not find any spatial variation in hunting mortality on the Tuscarora study area, I limited my hunting efficiency analysis to public land on the Sproul study area. A chorograph shows that hunting efficiency was not uniform across the landscape, indicating that deer were more vulnerable to harvest in some areas, regardless of hunting pressure at that location (Figure **4-21**).

Hunters were most efficient 500–1,000 m from a road and on moderate slopes between 10 and 20 degrees (Figures **4-22** and Figure **4-23**). Efficiency was below average far from roads and on both very flat and very steep slopes. Hunting efficiency increased with increasing hunter use except that efficiency was lowest in areas of highest hunter use (Figure **4-24)**.

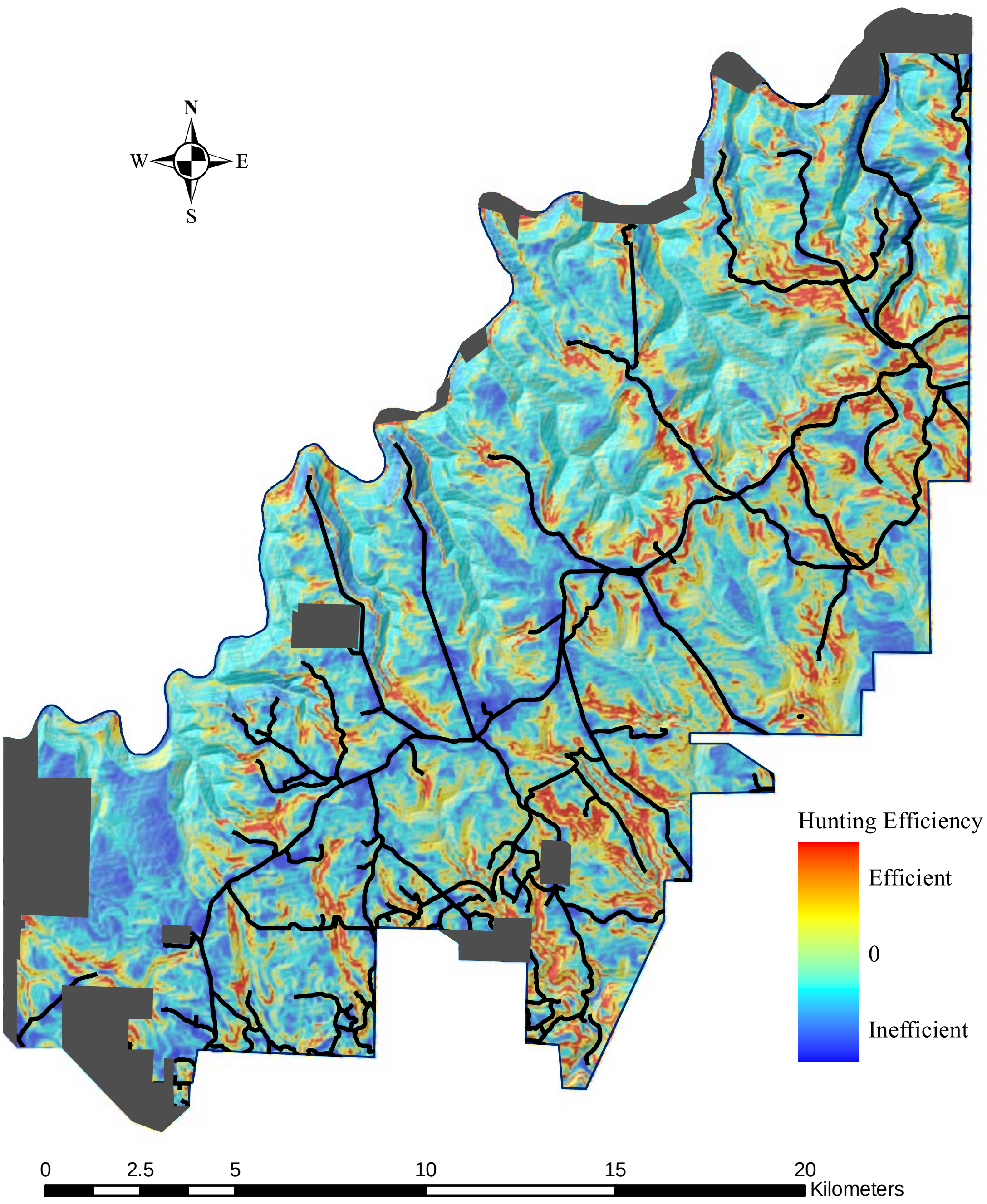

Figure **4-21**: Map representing hunting efficiency on the Sproul study area in north-central Pennsylvania, USA 2005-06. Black lines represent roads and gray shading represents private land. A hunting efficiency value of zero indicates that the hunting mortality rate and hunter use were both at the mean level.

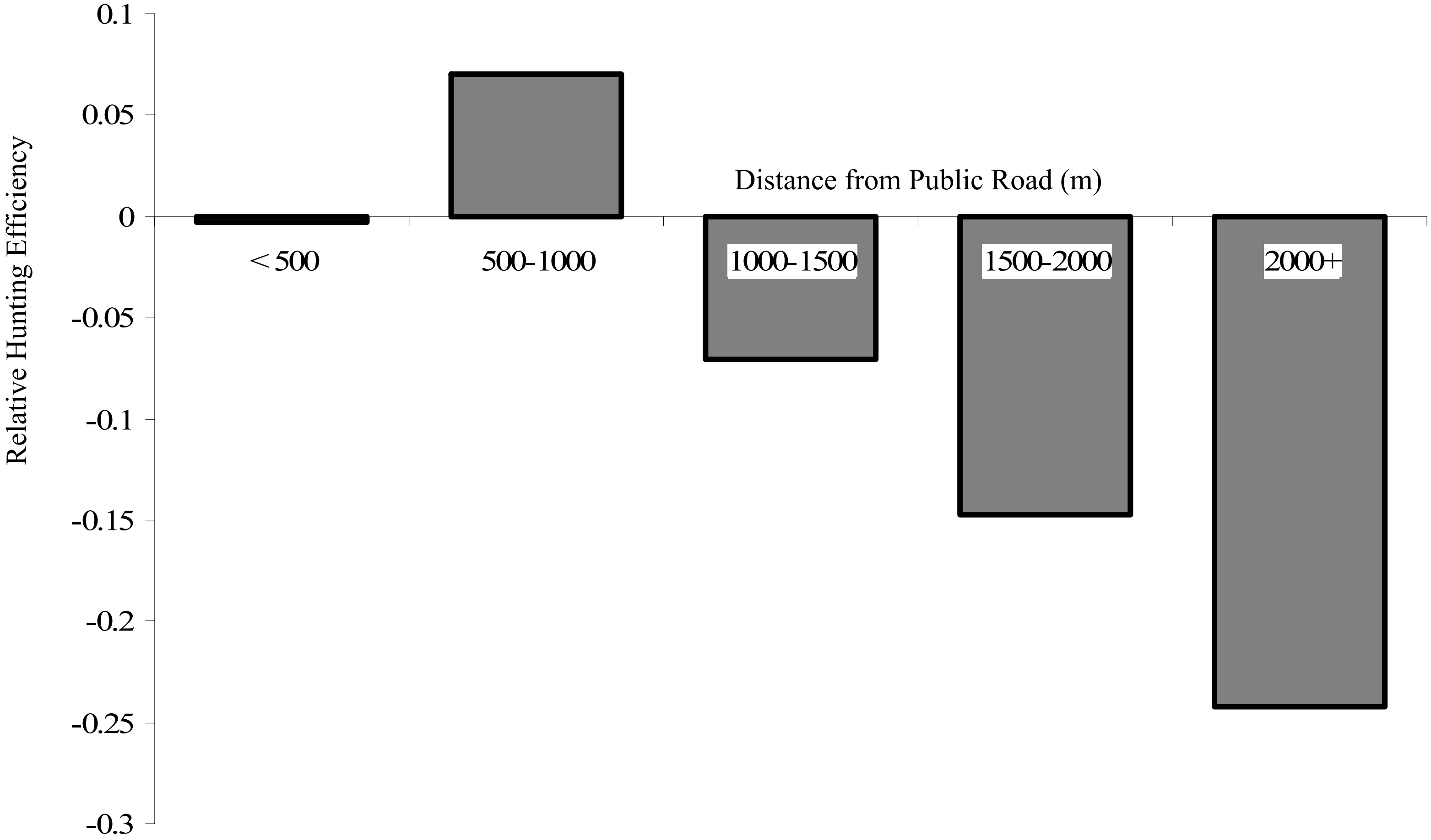

Figure **4-22**: Average hunter efficiency values for grid cells located within various categories of distance from the nearest road on the Sproul study area in north-central Pennsylvania, USA, 2005-06. A hunting efficiency value of zero indicates that the hunting mortality rate and hunter use were both at the mean level.

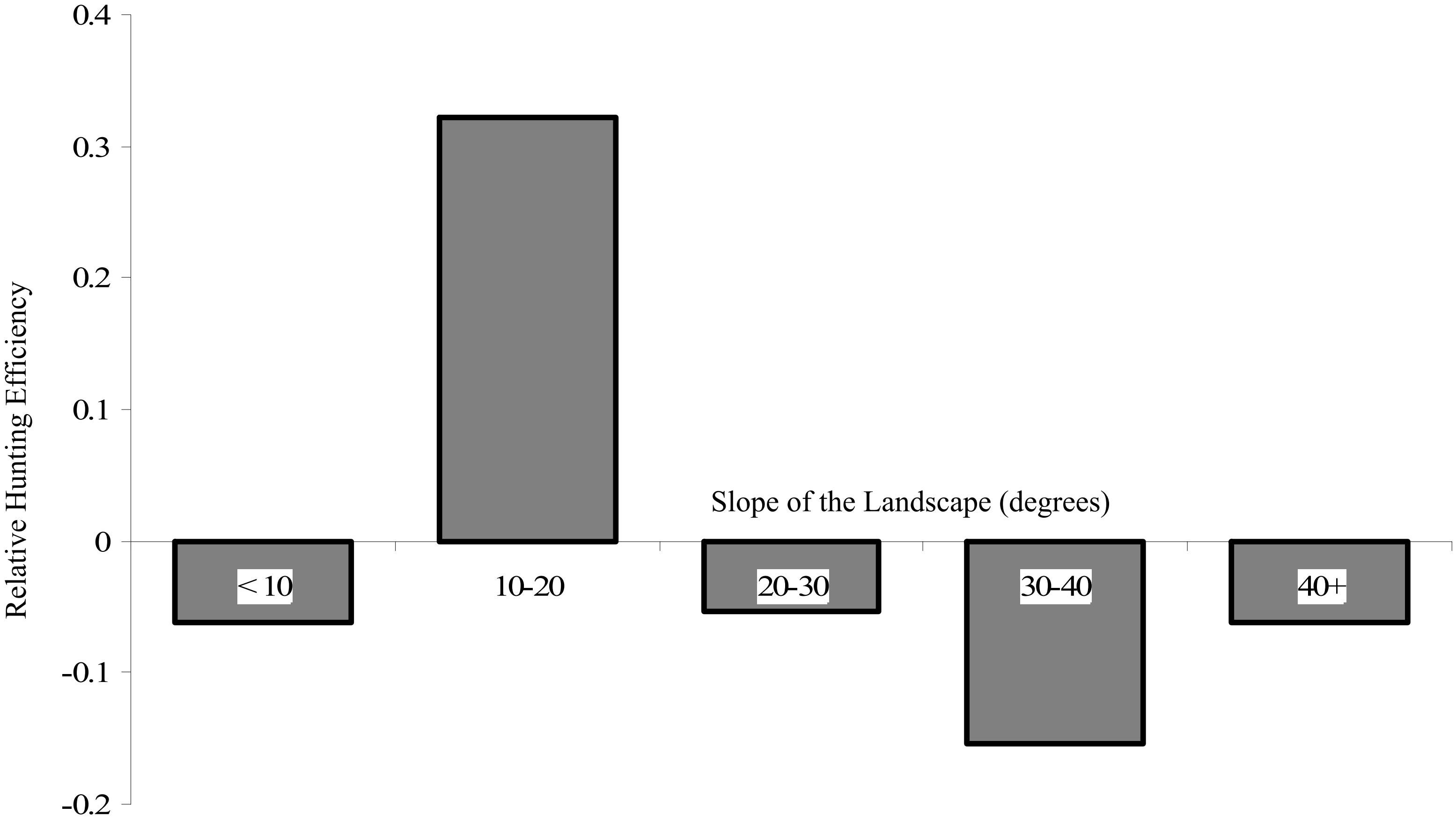

Figure **4-23**: Average hunter efficiency values for grid cells located within various slope categories on the Sproul study area in north-central Pennsylvania, USA, 2005-06. A hunting efficiency value of zero indicates that the hunting mortality rate and hunter use were both at the mean level.

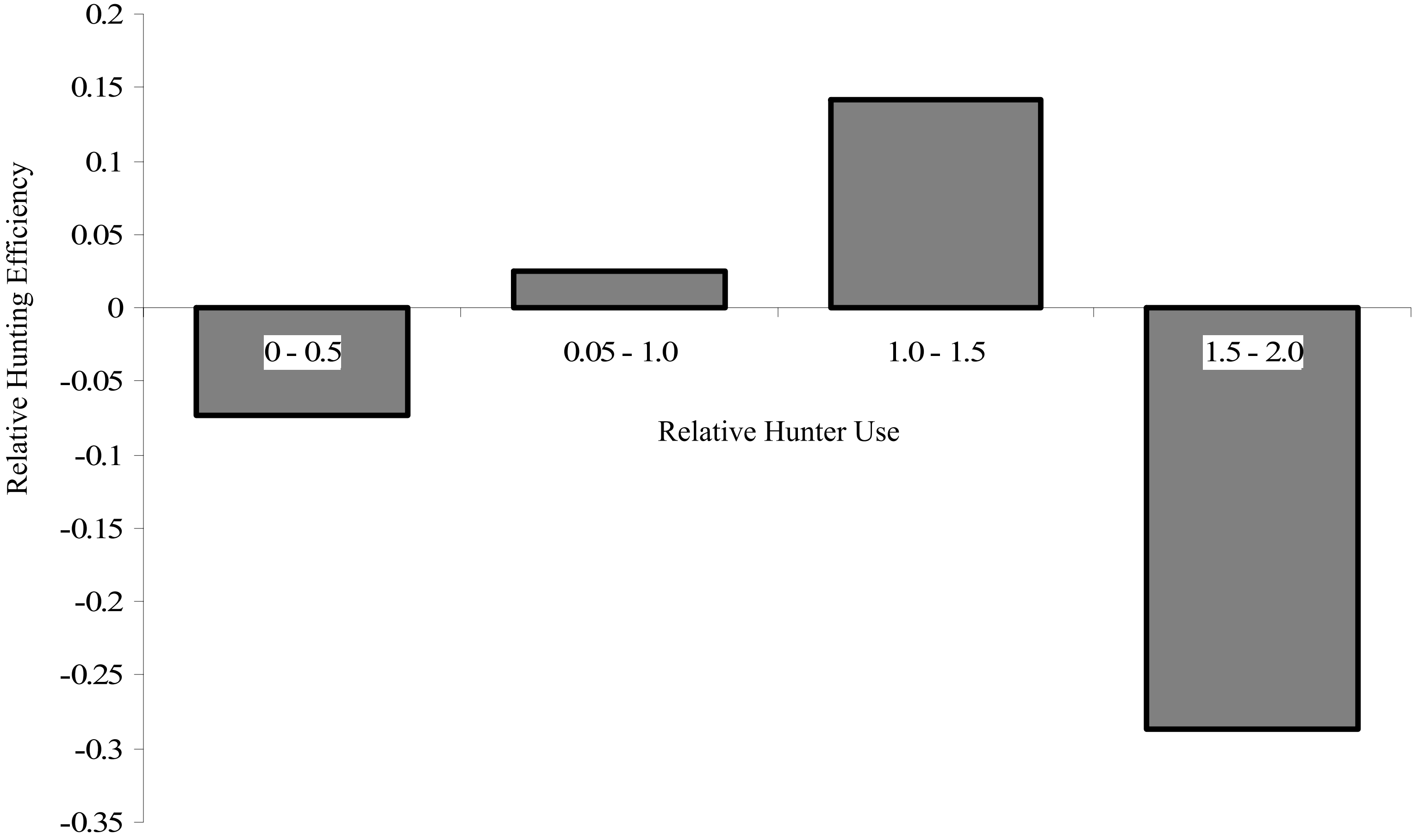

Figure **4-24**: Average hunting efficiency values for grid cells located within various hunter use categories on the Sproul study area in north-central Pennsylvania, USA, 2005-06. A hunting efficiency value of zero indicates that the hunting mortality rate and hunter use were both at the mean level.

Predicted changes in hunting mortality and refugia

Expanding the road network on the Sproul study area to include all gated and unimproved roads would increase the hunting mortality rate from 5.71% to 6.84% (19.9% change), and reduce the size of *de facto* refugia on the study area from 4,225 ha to 2,713 ha (-67.3% change).

Chapter 5

Discussion

Estimation bias

Deer that I lost contact with via telemetry during the hunting season were classified as legal harvests, which may have overestimated the harvest rate. Also, I assumed that all radio-collars 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, I know that some hunters who legally harvested deer refused to cooperate and destroyed or removed radio-collars from the study area. Consequently, I believe the few radio-collars that went missing during the hunting season represent legally harvested deer.

A survey of hunters who participated in the DMAP program on the study areas indicated that some hunters would be reluctant to harvest radio-collared deer even if it were legal to do so (PGC, unpublished data). These findings suggest that radio-collared deer may have been harvested at a lower rate than other deer, resulting in underestimated harvest rates and overestimated annual survival. However, an earlier study in Pennsylvania compared harvest rates of male white-tailed deer fitted with ear-tag transmitters (that are difficult to see) and radiocollars and found no statistical difference in harvest rates (E.S. Long, unpublished data; D.R. Diefenbach, personal communication). Also, the low harvest rates in Sproul are consistent with data indicating that some of the oldest deer harvested in Pennsylvania are from WMU 2G, suggesting that deer in this area experience lower harvest rates (PGC, unpublished data).

In light of potential bias in harvest and survival rates, these estimates should be interpreted with caution. However, analysis of the spatial and demographic differences in harvest rate, and the spatial distribution of hunting mortality should not be affected by such bias.

Annual survival

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 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.

Annual survival did not differ between adults and subadults, indicating that once female deer survive to one year of age they have similar survival rates as older deer. This is consistent with published research comparing survival rates between subadults and adults (Nelson and Mech 1986, Dusek et al. 1992, Van Deelen et al. 1997). However, my *a priori* list of candidate models did not include an AGE*Site interaction term because I assumed that any age effect would be consistent between study sites. Because harvest rate varied between adults and subadults on the Tuscarora study site, it is possible that annual survival also varied by age of deer at that location. My finding that hunting is the greatest source of mortality to deer also is consistent with published literature (Dusek 1989, Fuller 1990, Dusek et al. 1992, Whitlaw et al. 1998).

Harvest rate

The estimated 4.4% harvest rate on public lands in the Sproul study area was lower than rates observed in other studies. However, the harvest estimate for private land on the Sproul study area was four times greater and consistent with published research (Dusek 1989, Fuller 1990, Dusek et al. 1992, DelGiudice et al. 2002). 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. My results on the spatial distribution of hunters and hunting mortality support this hypothesis.

The lower harvest rates also may be related to hunter attitudes. Hunters in the Sproul study area who hunt solely on public land are more reluctant to harvest female deer than hunters who also hunt private land (Stedman et al. 2008). This difference in harvest rates between public and private portions of the study area indicated that harvest rates can vary greatly within a WMU.

The similar harvest rates on public and private land on the Tuscarora study area may be because the road network facilitated easier retrieval of harvested game from rugged areas than in Sproul.

Hunter density

Hunter density estimates for public land on the Sproul study area were similar to results from previous studies conducted by Stedman et al. (2004) and Diefenbach et al. (2005) on the same study area. However, this study provided estimates of hunter density during opening morning of rifle season, likely the day of maximum hunting activity, and also estimated density on adjoining private land. Also I estimated hunter density and distribution in the Ridge and Valley province of Pennsylvania, allowing comparison between regions with different topography and road network configurations.

Hunter density on both study areas generally declined after the first two days, then increased on both Saturdays. This trend is consistent with published literature (Fuller 1988, Stedman et al. 2004, Diefenbach et al. 2005). I found evidence of a shift in hunter density between public and private land on 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 during this time period, whereas hunter density on the Tuscarora study area increased on public land and decreased on private land. Hunting parties that harvest fewer deer may be more likely to quit hunting or change location than parties that harvest more deer. Changes in hunter use also may be a function of hunter behavior patterns, such as traditions of hunting in particular locations on opening morning. More research on hunter behavior is needed to understand the changes I observed in hunter density.

Spatial distribution of hunters and hunting mortality

Estimates of hunter distribution on public lands in the Sproul study area were consistent with previous research conducted in the same location (Stedman et al. 2004, Diefenbach et al. 2005); most hunters remained close to roads and on flat slopes. I found that hunters on public land in the Tuscarora study area exhibited a similar preference for locations close to roads. These results are consistent with research conducted in northern Minnesota where few hunters traveled far from roads (Fuller 1988). On private lands in both study areas I found a more uniform distribution of hunters with respect to distance from roads. Because use of vehicles on private land is not regulated except by the landowner, hunters likely had access to most of the landscape. Slightly fewer hunters were found close to roads on private land on the Tuscarora study area, likely because these areas were not forested and unlikely to be good hunting areas for deer.

Hunters on both public and private land in the Sproul study area preferred to hunt on flatter terrain. Hunters in the Tuscarora study area, however, exhibited very little preference with regard to slope, possibly because the road network in Tuscarora traverses both high and low elevations, so deer harvested on steep slopes could be dragged downhill to a road. Most public roads in the Sproul study area were located on flat, high elevation plateaus; deer harvested in steep drainages must be transported uphill to the nearest road.

Hunting mortality rate in the Sproul study area was highest close to roads, likely because hunter use was concentrated in those areas. Slope of the landscape, however, had very little influence on hunting mortality even though fewer hunters used steep slopes, indicating that hunting mortality was not necessarily proportional to hunter use.

A map of relative hunting efficiency showed mortality was quite variable throughout the landscape, even when corrected for hunter use. Hunters that used moderate slopes were more likely to kill deer than hunters on flatter terrain. However, hunting efficiency was lower at the steepest slopes and very far from roads. Hunters in such rugged terrain may have been targeting antlered deer. Bhandari et al. (2006) concluded that "harvesting of antlered deer [on the Sproul State Forest] was more a matter of effort than motive", suggesting that hunters pursuing antlered deer may be more likely to simply exert the effort required to hunt in rugged remote locations. Spatial variation in hunting efficiency also may have been a reflection of hunter distribution. The chance of an individual hunter harvesting a deer (hunting efficiency) was greatest in areas of moderate hunter use and efficiency was lowest in areas that received the most hunting pressure. This pattern may be related to deer behavior in response to hunter density or that a limited number of deer may result in lower hunter success rates at very high hunter densities.

Locations far from roads and on very steep slopes in the Sproul study area received very little hunting pressure. Further, the few hunters that used such areas were less likely to kill an antlerless deer than hunters that occupied more accessible terrain. As a result, several large portions of the study area experienced hunting mortality rates of <2%, serving 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). Extended hunting seasons and increased permit allocation could have minimal effect on deer population dynamics in these areas.

Improving hunter access to areas with refugia may be the most effective way to control local deer populations. Several roads on the Sproul study area have been decommissioned or gated and closed to public hunters. Opening these roads during hunting season would reduce the amount of *de facto* refugia on the study area by 67%.

Land managers also could increase hunter access to remote areas by constructing new roads or permitting use of all-terrain vehicles. Results from this research indicated that such changes may increase both the number of hunters and individual hunter success.

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Appendix

Hunter Observation Detection Functions

Sproul study area – 2005

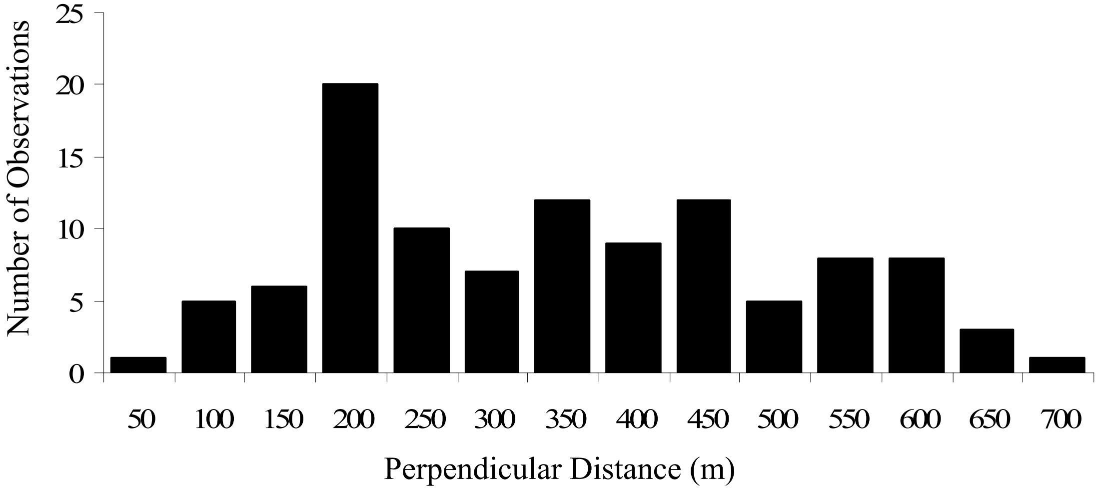

Figure **A-1**: Histogram of all hunter observations vs. distance from flight path for observer 1 on Sproul study area, Pennsylvania, 2005. Observations <125 meters from the flight path were difficult to detect, and were discarded from further analysis.

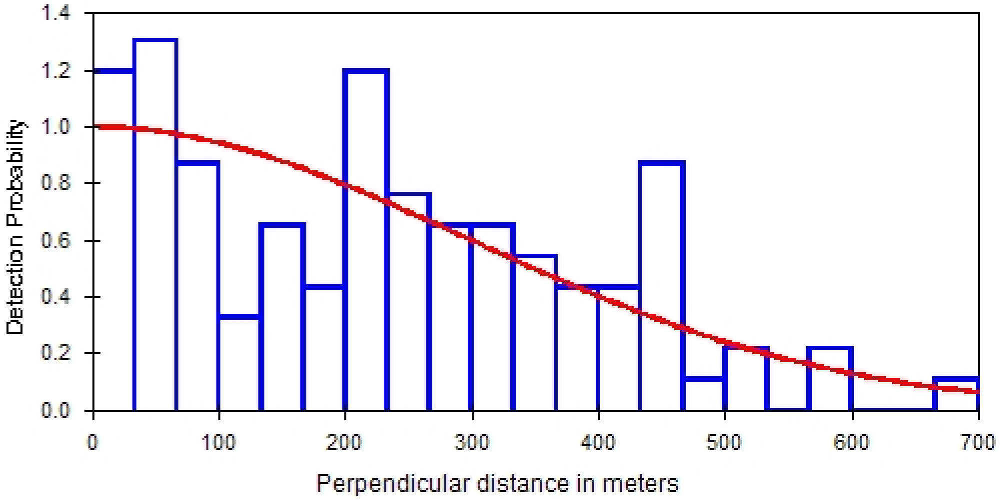

Figure **A-2**: Histogram of hunter observations and probability of detection (line) as a function of distance from observer 1 on the Sproul study area, Pennsylvania, 2005. Observations were left-truncated at 125 meters.

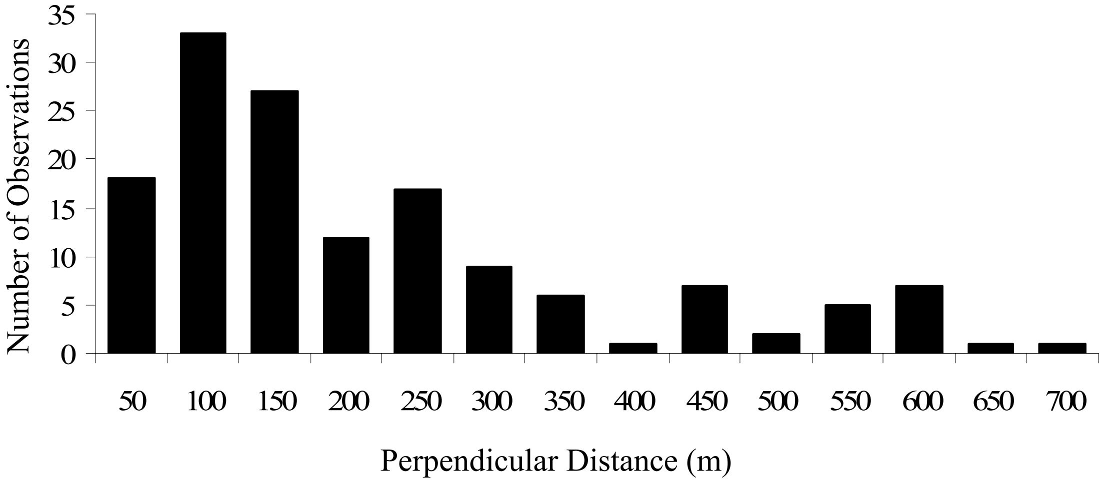

Figure **A-3**: Histogram of all hunter observations vs. distance from flight path for observer 2 on Sproul study area, Pennsylvania, 2005. Observations <75 meters from the flight path were difficult to detect, and were discarded from further analysis.

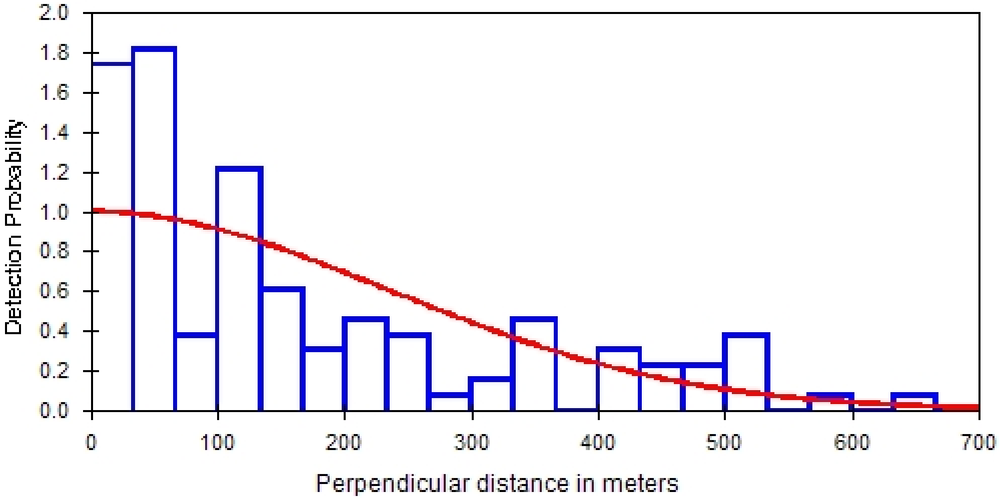

Figure **A-4**: Histogram of hunter observations and probability of detection (line) as a function of distance from observer 2 on public land, Sproul study area, Pennsylvania, 2005. Observations were left-truncated at 75 meters.

Tuscarora study area – 2005

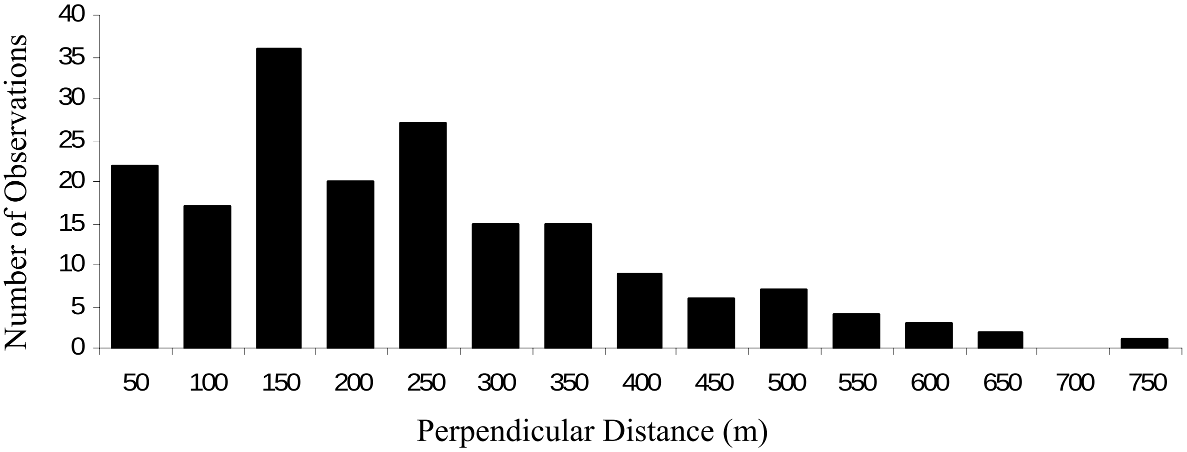

Figure **A-5**: Histogram of all hunter observations vs. distance from flight path for observer 1 on Tuscarora study area, Pennsylvania, 2005. Observations <80 meters from the flight path were difficult to detect, and were discarded from further analysis.

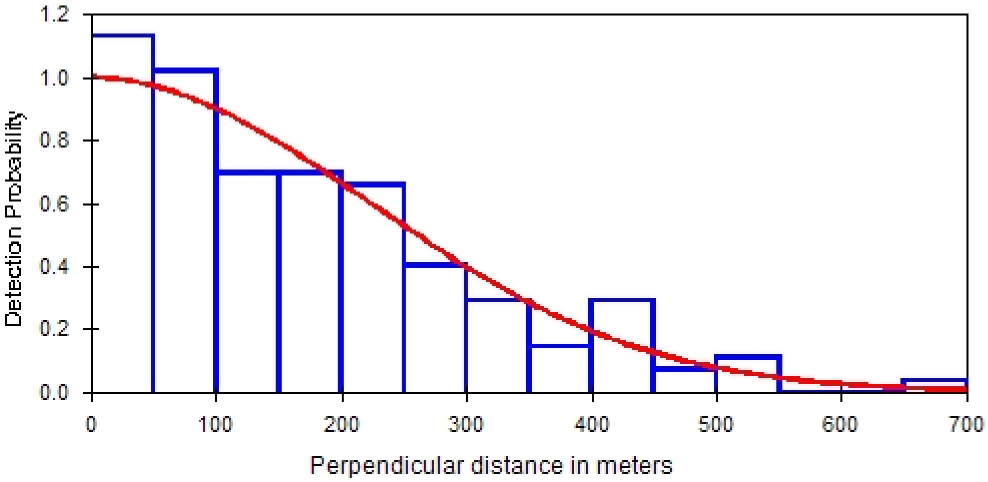

Figure **A-6**: Histogram of hunter observations and probability of detection (line) as a function of distance from observer 1 on the Tuscarora study area, Pennsylvania, 2005. Observations were left-truncated at 80 meters.

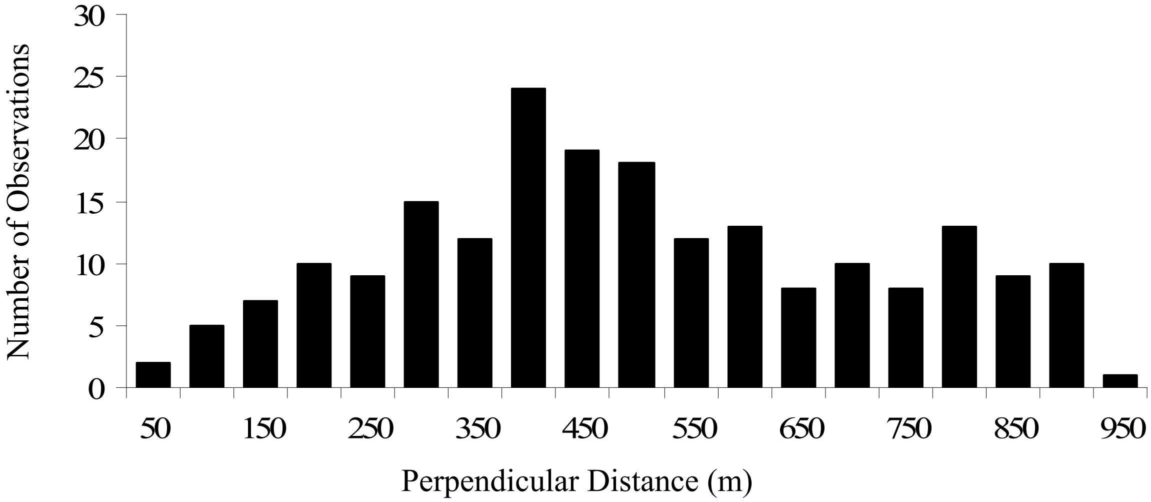

Figure **A-7**: Histogram of all hunter observations vs. distance from flight path for observer 2 on Tuscarora study area, Pennsylvania, 2005. Observations <320 meters from the flight path were difficult to detect, and were discarded from further analysis.

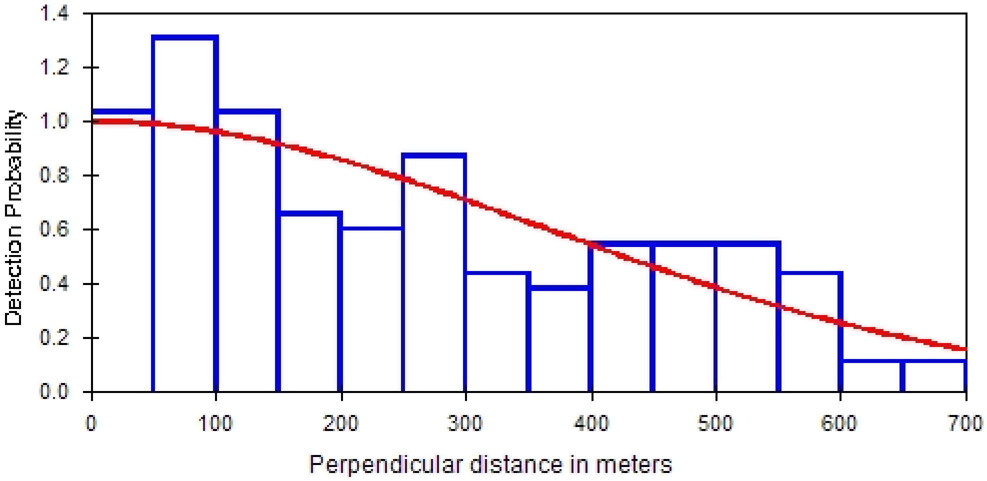

Figure **A-8**: Histogram of hunter observations and probability of detection (line) as a function of distance from observer 2 on the Tuscarora study area, Pennsylvania, 2005. Observations were left-truncated at 320 meters.

Sproul study area – 2006

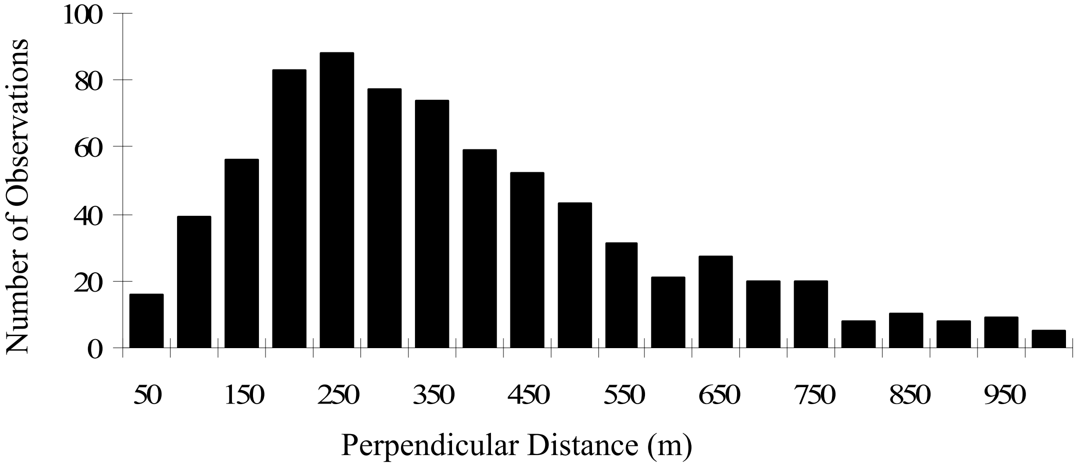

Figure **A-9**: Histogram of all hunter observations vs. distance from flight path for observer 1 on Sproul study area, Pennsylvania, 2006. Observations <180 meters from the flight path were difficult to detect, and were discarded from further analysis.

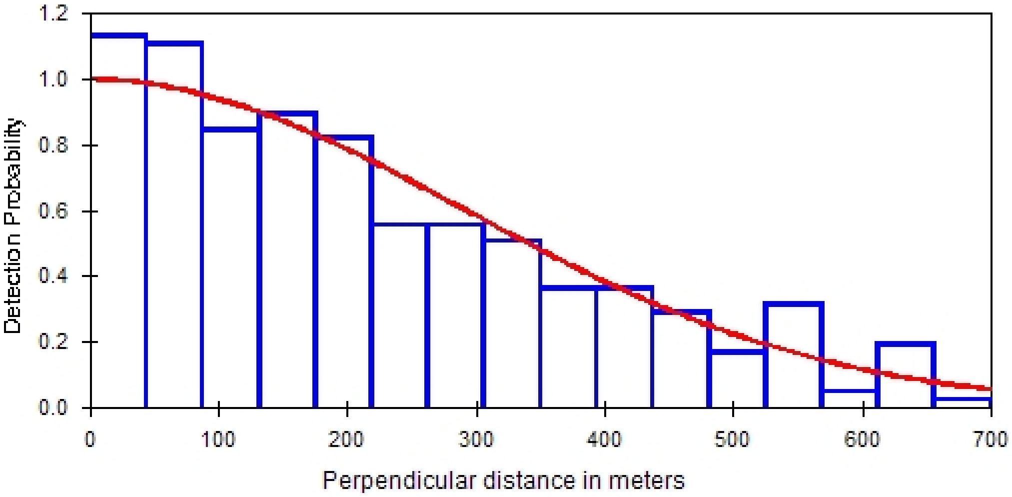

Figure **A-10**: Histogram of hunter observations and probability of detection (line) as a function of distance from observer 1 on public land, Sproul study area, Pennsylvania, 2006. Observations were left-truncated at 180 meters.

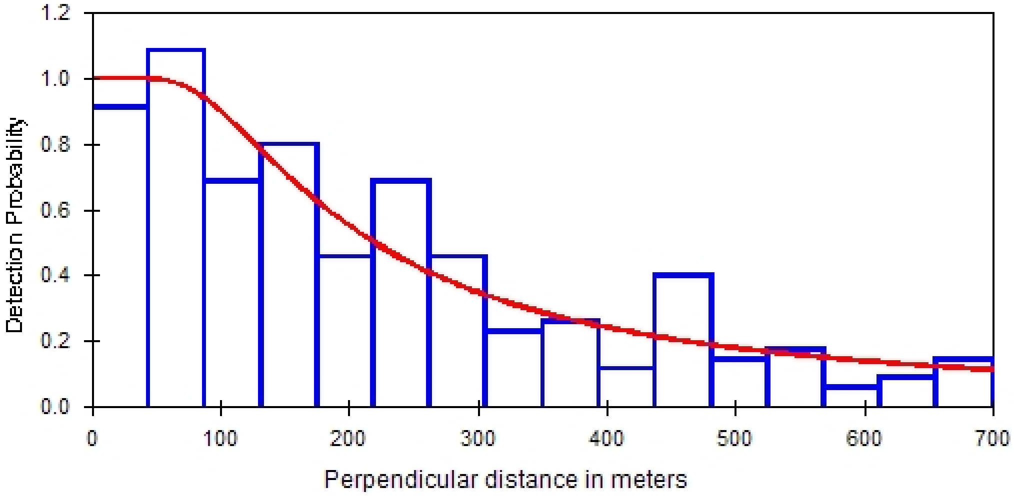

Figure **A-11**: Histogram of hunter observations and probability of detection (line) as a function of distance from observer 1 on private land, Sproul Study Area, Pennsylvania, 2006. Observations were left-truncated at 180 meters.

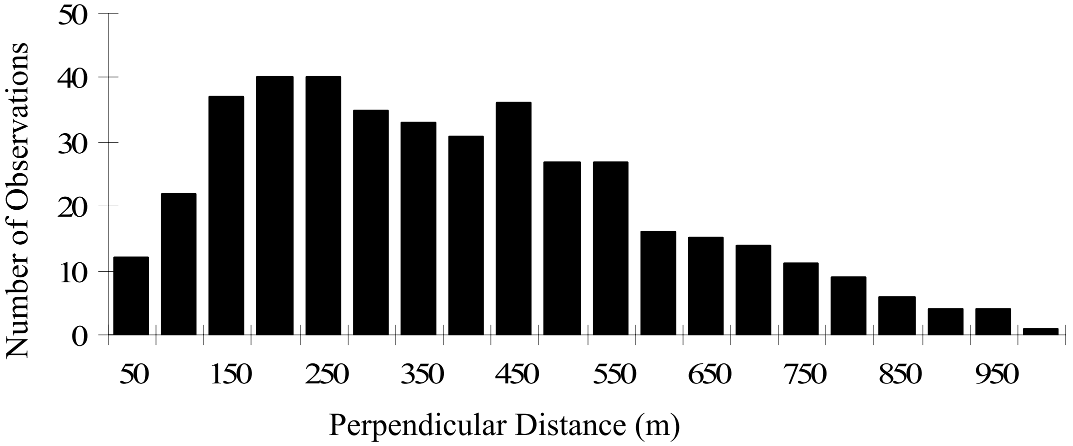

Figure **A-12**: Histogram of all hunter observations vs. distance from flight path for observer 2 on Sproul study area, Pennsylvania, 2006. Observations <110 meters from the flight path were difficult to detect, and were discarded from further analysis.

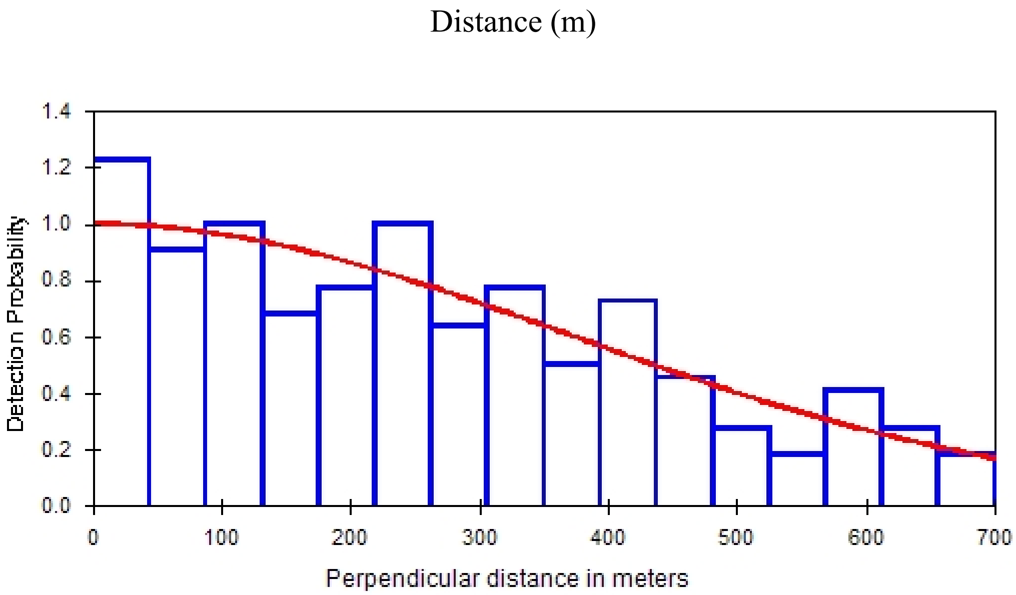

Figure **A-13**: Histogram of hunter observations and probability of detection (line) as a function of distance from observer 2 on public land, Sproul study area, Pennsylvania, 2006. Observations were left-truncated at 110 meters.

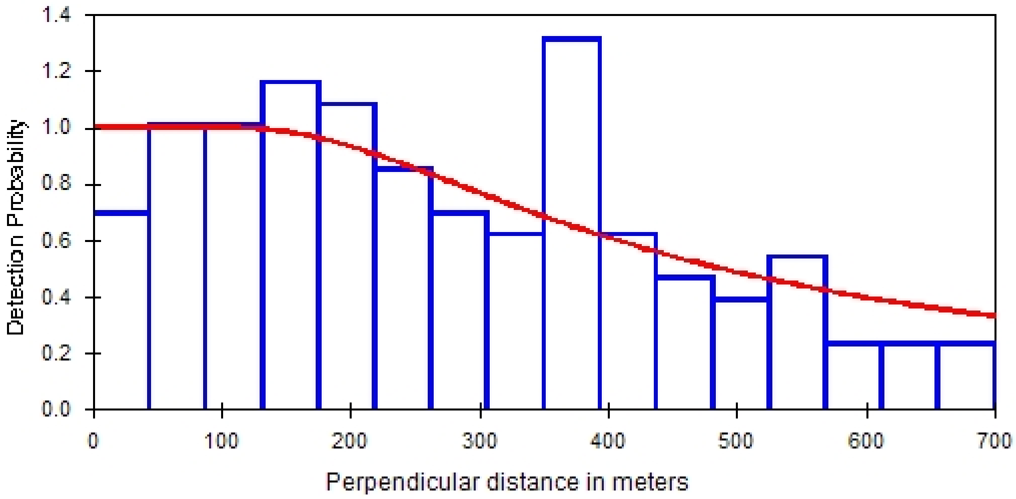

Figure **A-14**: Histogram of hunter observations and probability of detection (line) as a function of distance from observer 2 on private land, Sproul study area, Pennsylvania, 2006. Observations were left-truncated at 110 meters.

Tuscarora study area – 2006

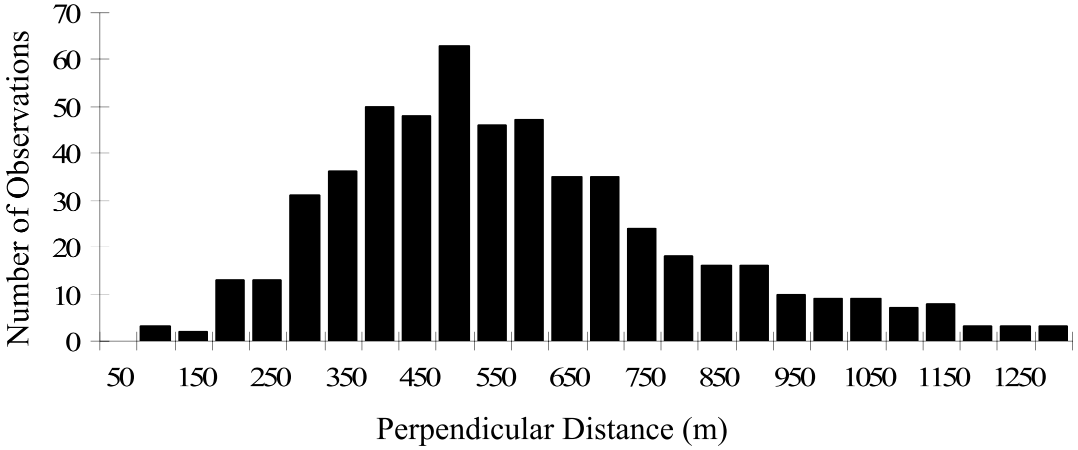

Figure **A-15**: Histogram of all hunter observations vs. distance from flight path for observer 3 on Tuscarora study area, Pennsylvania, 2006. Observations <400 meters from the flight path were difficult to detect, and were discarded from further analysis.

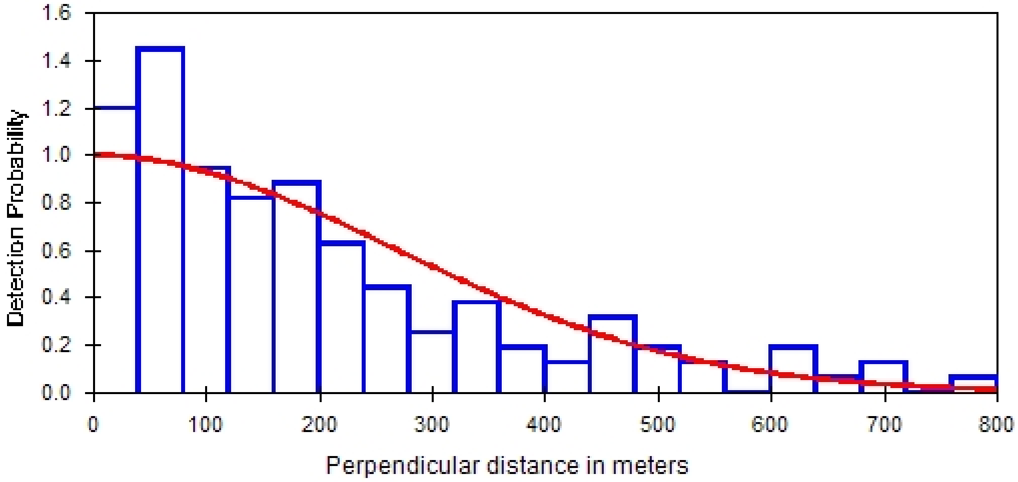

Figure **A-16**: Histogram of hunter observations and probability of detection (line) as a function of distance from observer 3 on public land, Tuscarora study area, Pennsylvania, 2006. Observations were left-truncated at 400 meters.

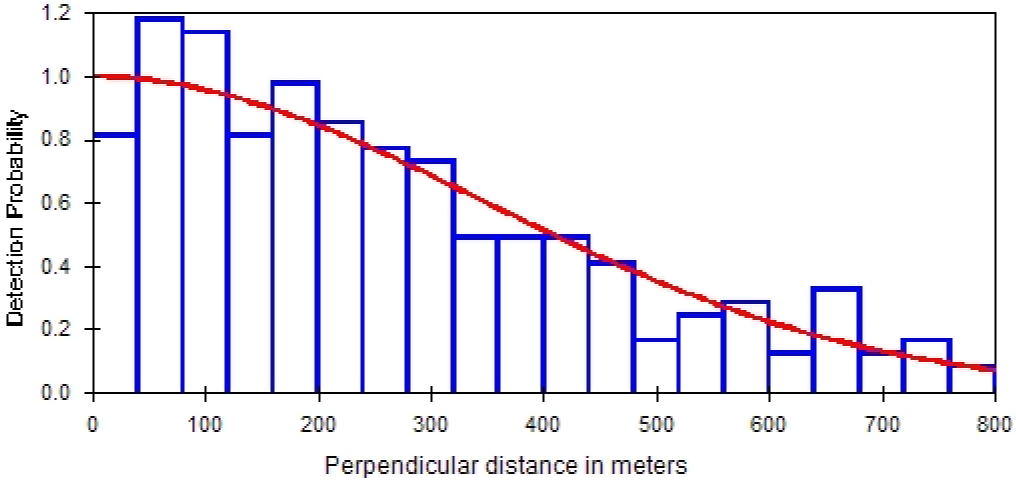

Figure **A-17**: Histogram of hunter observations and probability of detection (line) as a function of distance from observer 3 on private land, Tuscarora study area, Pennsylvania, 2006. Observations were left-truncated at 400 meters.

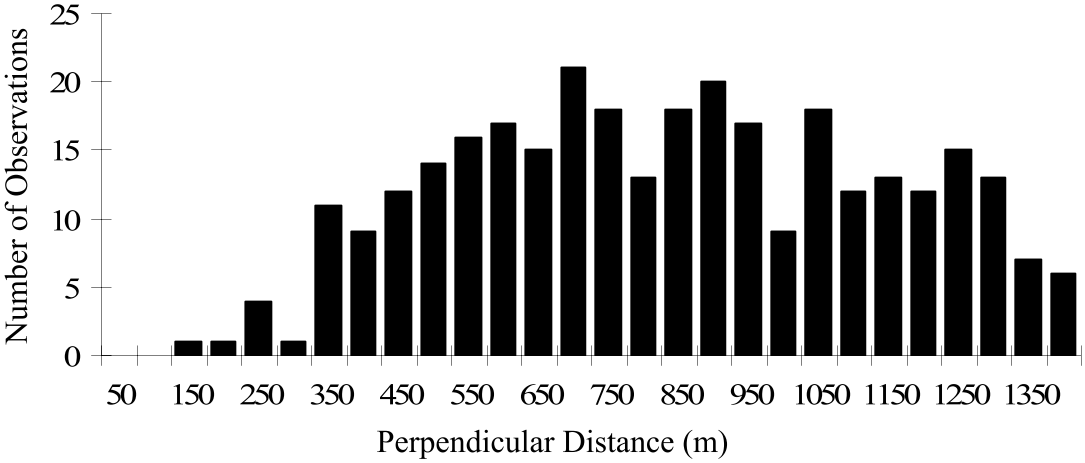

Figure **A-18**: Histogram of all hunter observations vs. distance from flight path for observer 4 on Tuscarora study area, Pennsylvania, 2006. Observations <600 meters from the flight path were difficult to detect, and were discarded from further analysis.

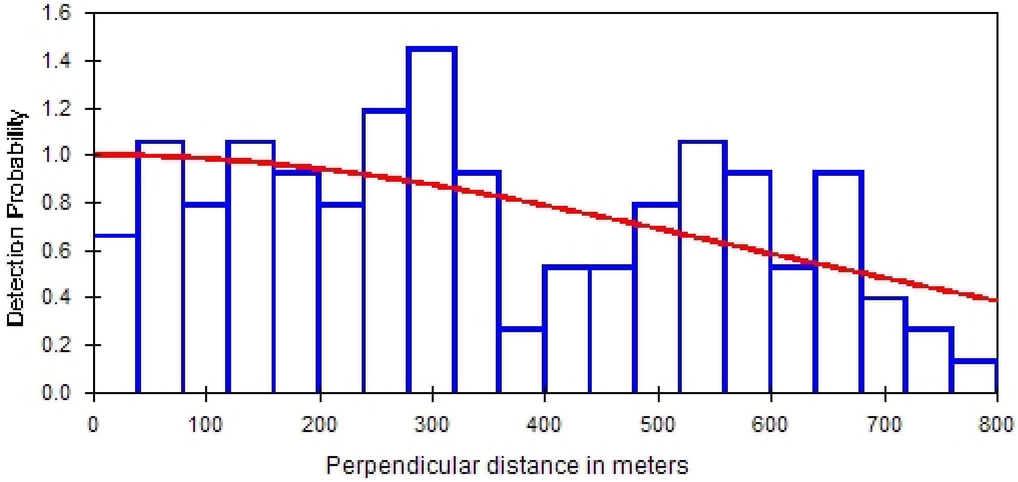

Figure **A-19**: Histogram of hunter observations and probability of detection (line) as a function of distance from observer 4 on public land, Tuscarora study area, Pennsylvania, 2006. Observations were left-truncated at 600 meters.

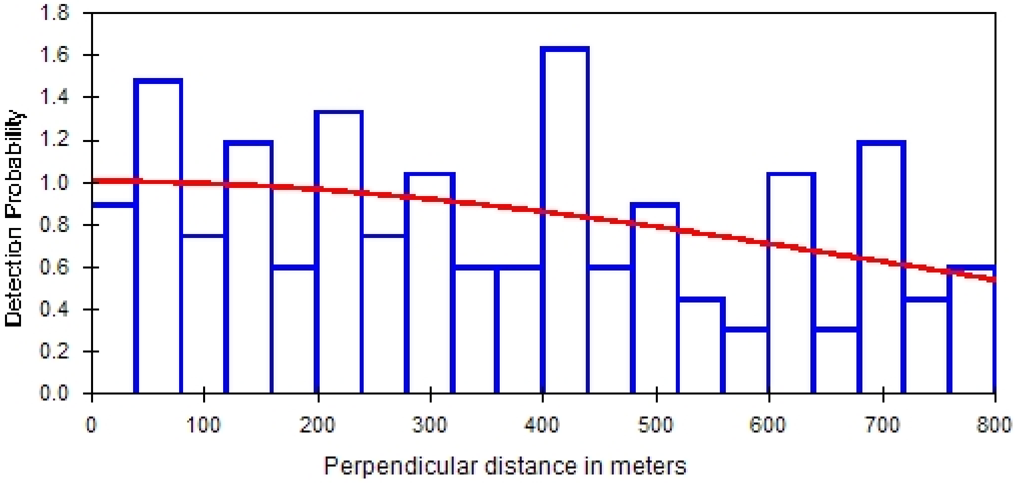

Figure **A-20**: Histogram of hunter observations and probability of detection (line) as a function of distance from observer 4 on private land, Tuscarora study area, Pennsylvania, 2006. Observations were left-truncated at 600 meters.